The Growth Rate of the American Lobster (Homarus americanus)

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(Received for publication December 16, 1952)

ABSTRACT

Carapace measurements of lobster larvae caught in the western part of Northumberland Strait showed that in this area the natural growth in length per moult is 34.4 per cent from stage 1 to stage 2, 31.8 per cent from stage 2 to 3, and 30.3 per cent from stage 3 to 4. The seasonal distribution of the first four larval stages was determined from plankton tows made continuously from mid-June to late September each year from 1948 to 1952. To determine natural annual growth, lobsters of 15 to 25 cm., total length, were sorted into five or six size groups and were distinctively marked by means of holes punched through the tail fan. These were liberated on six widely separated fishing grounds in the Maritime Provinces. Recoveries of these marked lobsters four to twelve months after release showed that in the southern Gulf of St. Lawrence, 15- to 20-cm. lobsters grew 8 to 9 mm. (13 to 15 per cent) in carapace length, 22 to 25 mm. (13 to 14 per cent) in total length and 80 to 95 grams (45 to 53 per cent) in weight. In southern Nova Scotia and Grand Manan 20- to 25-cm. lobsters grew 10 to 12 mm. (13 to 15 per cent) in carapace length, 27 to 34 mm. (12 to 15 per cent) in total length and 170 to 220 grams (43 to 54 per cent) in weight. From the carapace length of 4th-stage larvae and straight-line equations relating carapace length before moulting and carapace length after moulting, the average carapace lengths of lobsters in stages 5 to 20 were calculated. From observations and calculations on the growth per moult and moulting frequency, it is estimated that in the Northumberland Strait area lobsters reach a length of 14 cm. (5½ in.) at the end of the fifth growing season (4¼ years old) and 24 cm. (9½ in.) at the end of the ninth growing season (8¼ years).

INTRODUCTION

The recaptures of tagged lobsters which have been liberated in Canadian waters have shown the fishery to be intensive, 40 to 80 per cent of the tags being returned each season (Wilder, 1947). To maintain production from this intensive fishery, minimum size limits have been generally adopted. Several different minima were established for different areas in relation to the size composition of the lobster stocks and some changes in the limits have been made on a trial-and-error basis. To date, however, calculation of the best minimum size limits to ensure the maximum sustained yield has been impossible because of inadequate knowledge of growth and natural mortality rates.

Herrick (1896), largely on the basis of lobsters reared under artificial conditions at Woods Hole, Massachusetts, made the first systematic attempt to determine the growth and age of the American lobster. Later Hadley (1906), with more extensive material available, published growth estimates based principally on lobsters reared artificially at Wickford, Rhode Island. Except for the work of Templeman (1936a, 1948b) and Wilder (1948) almost no new growth data

J. Fish. Res. Bd. Can., 10(7), 1953.
Printed in Canada.

pertaining to the American lobster have been published, and Hadley's estimate has continued to be generally accepted.

With an animal such as the lobster which has neither scales, otoliths, vertebrae nor fin rays, which at each moult loses all hard parts (including external tags), and which over the size range normally captured does not fall into recognizable size or age groups, the estimation of growth and age is particularly difficult. In the present paper data are presented on the seasonal occurrence and natural growth per moult of lobster larvae captured in Northumberland Strait and on the growth of larger lobsters marked and liberated on various fishing grounds.

ACKNOWLEDGMENTS

The writer acknowledges with pleasure the valuable assistance of Technicians L. G. Kervin, R. C. Murray, G. J. W. Sullivan, U. J. Walsh and W. W. Yorston, who carried out the extensive field work involved in the marking experiments. The systematic towing for lobster larvae was conducted by Captains Jules LeBlanc, H. H. Butler, A. L. Outhouse and L. I. Cross. Captain A. E. Calder designed the special plankton net and provided general assistance. The bottom drag designed by H. Y. Brownrigg to capture the early bottom stages was operated successfully by Captain L. I. Cross to obtain what is believed to be the first collection of these sizes from nature. The enthusiastic co-operation and interest of many lobster fishermen and dealers which greatly facilitated the field work are very much appreciated.

SEASONAL OCCURRENCE OF LOBSTER LARVAE

In June 1948 a program of systematic surface towing for lobster larvae was initiated in the northern part of Northumberland Strait between Richibucto, New Brunswick, and Miminegash, Prince Edward Island. A series of 23 stations, approximately 2½ nautical miles (4.6 km.) apart were established as illustrated in Figure 1. At each of these stations, when weather and facilities permitted, half-hour daylight surface tows were made with a net especially designed for this purpose. The net which was made of no. 16 grit gauze (16 meshes to the inch) was approximately 25 feet (7.6 metres) long, tapering from 12×3 feet. (3.7×0.9 m.) at the mouth to a diameter of 10 inches (25 cm.). The mouth of the net was held open by a framework of ¾-in. (19-mm.) galvanized pipe. Since as shown by Templeman (1937, 1945) lobster larvae are concentrated near the surface during daylight hours, floats made of 5-gallon (23-litre) steel oil drums were attached to the framework to ensure that part of the net mouth was above the surface at all times (Figure 2). Each year from 1948 to 1952 towing has been continued from June to September. During this period 1,599 tows have been made in which a total of over 70,000 lobster larvae have been caught. The total catch of larvae for these five years is listed by half-monthly periods in Table I together with the average catch per tow.

These data show that in this area lobster hatching continues at a relatively high level from mid-June to the end of August.

TABLE I. Number of 30-minute plankton tows made off Richibucto, N.B., from 1948 to 1952, by half-monthly periods; number of larvae caught; and average catch per tow.

Period	Number of tows	Number of larvae				Catch per tow			
		Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
June 1–15	57	0	0	0	0	0	0	0	0
16–30	193	4,125	105	1	0	21.37	0.54	0.01	0
July 1–15	250	15,516	2,671	473	92	62.06	10.68	1.89	0.37
16–31	273	11,629	3,026	1,505	1,599	42.60	11.08	5.51	5.86
Aug. 1–15	260	15,017	3,061	1,776	1,233	57.76	11.77	6.83	4.74
16–31	264	5,357	2,038	1,312	1,025	20.29	7.72	4.97	3.88
Sept. 1–15	196	709	154	109	126	3.62	0.78	0.56	0.64
16–30	106	50	4	3	19	0.47	0.04	0.03	0.18
Totals	1,599	52,403	11,059	5,179	4,094				

Fourth-stage larvae first appeared in the tows during the first half of July and were relatively abundant from mid-July to the end of August.

LARVAL GROWTH PER MOULT

The growth per moult of larvae reared under artificial conditions at Woods Hole, Massachusetts, and Wickford, Rhode Island, has been determined by Herrick (1896) and Hadley (1906) as indicated in Table II.

TABLE II. Average size and growth per moult of lobster larvae reared at Woods Hole, Mass., and Wickford, R.I., according to Herrick and Hadley.

	Woods Hole (Herrick)			Wickford (Hadley)		
	Total length	Growth		Total length	Growth	
	mm.	mm.	%	mm.	mm.	%
Stage 1	7.84			8.2		
		1.36	17.4		1.4	17.1
Stage 2	9.20			9.6		
		1.9	20.6		1.8	18.8
Stage 3	11.1			11.4		
		1.5	13.5		2.1	18.4
Stage 4	12.6			13.5		

The following statements, "It could hardly be expected, moreover, that lobsters kept under artificial conditions would grow as rapidly as when free in the ocean" (Herrick, 1911) and ". . . when these young lobsters are isolated in glass dishes or other receptacles, for particular observation, the rate of growth does not appear to be the same as under natural conditions, but somewhat decreased" (Hadley, 1906), show that both of these workers believed growth would be somewhat greater in nature.

Templeman also questions growth records obtained under artificial con-

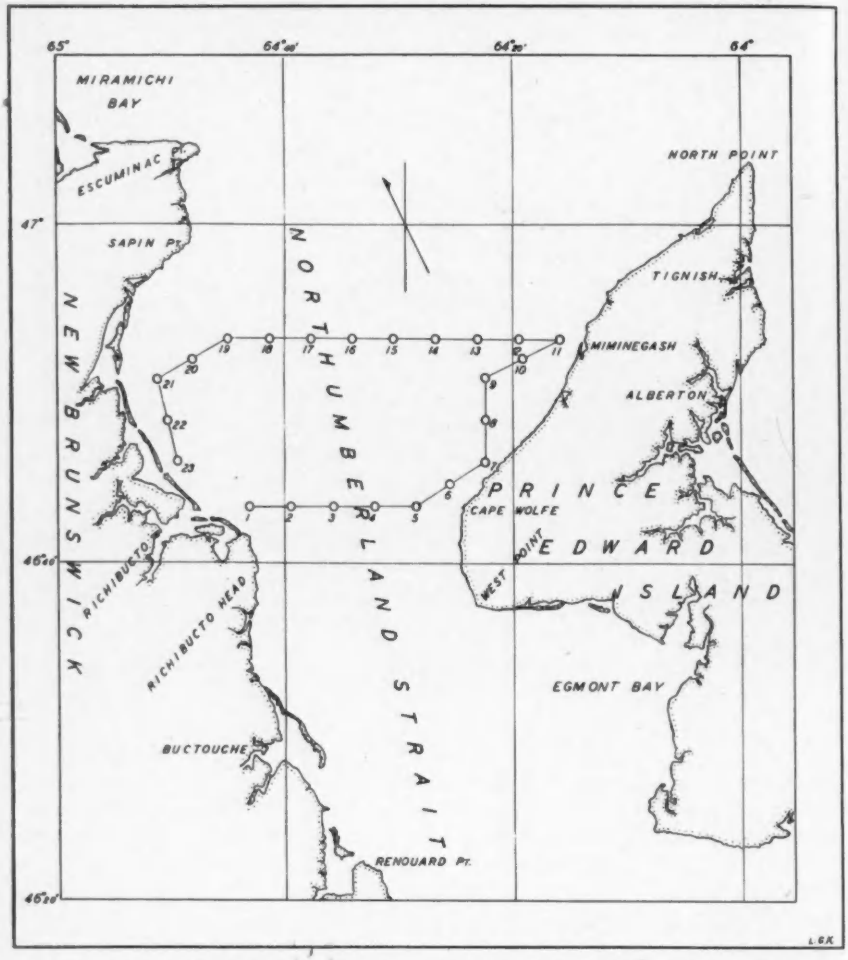

FIGURE 1. Stations at which towing for lobster larvae has been conducted from 1948 to 1952.

ditions, since he showed (Templeman, 1936a) that lobsters held in floats for up to six weeks prior to moulting grew considerably less than those which moulted within a few days of capture. He also pointed out in the same paper that carapace measurements give a more reliable indication of growth than total length, since for several days prior to the moult some stretching occurs at the junction of the cephalothorax and abdomen. In both larvae and adults, total length is difficult to measure accurately.

Templeman (1948b) presents data on the natural growth of lobster larvae caught in Bay of Islands and Notre Dame Bay, Newfoundland, which indicate that the growth per moult in carapace length varies from 32 to 37 per cent.

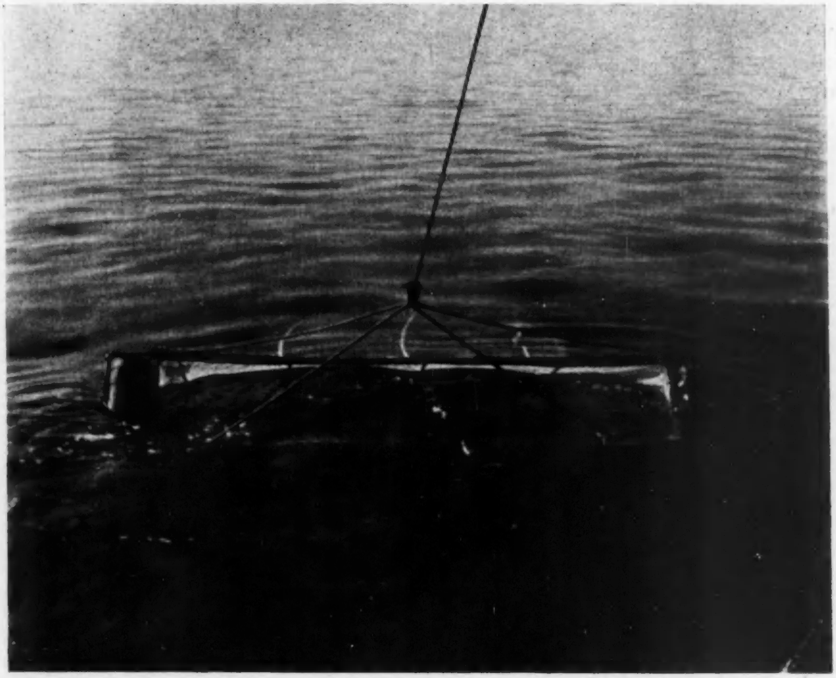

FIGURE 2. Lobster net being hauled in. (Photograph by National Film Board)

To determine the sizes and growth per moult of larvae caught in Northumberland Strait, a series of measurements was made on formalin-preserved larvae caught during August 1950. Carapace lengths from the posterior margin of the eye socket to the posterior end of the median dorsal line of the carapace were measured under a monocular microscope at a magnification of 12.4. This measurement was used by Templeman who, because of changes in the shape of the carapace during larval development, believed it to be more comparable to the measurement used for larger lobsters, which were measured from the posterior margin of the eye socket to the posterior margin of the carapace in a line parallel to the mid-dorsal line.

Templeman's data for Newfoundland larvae together with those obtained by the writer for Northumberland Strait larvae are presented in Table III.

Templeman (1936a, 1944b) has shown in areas of relatively high summer temperatures such as western Northumberland Strait that lobsters mature at smaller sizes. He suspected that these smaller mature lobsters might produce smaller eggs and 1st-stage larvae, and suggested that at these higher temperatures the growth per moult might be less than in colder areas such as Bay of Islands and Notre Dame Bay. According to Table III, larvae from Northumberland Strait do not differ consistently in size from those from the two Newfound-

TABLE III. Average carapace lengths and growth per moult of lobster larvae caught in Bay of Islands and Notre Dame Bay, Newfoundland, and in Northumberland Strait between Richibucto, N.B., and Miminegash, P.E.I.

	Bay of Islands (Templeman)				Notre Dame Bay (Templeman)				Northumberland Strait (Wilder)			
	No.	Cara-pace	Growth		No.	Cara-pace	Growth		No.	Cara-pace	Growth	
		mm.	*mm.*	%		*mm.*	*mm.*	%		*mm.*	*mm.*	%
Stage 1	107	1.81			65	1.89			50	1.92		
			0.65	35.9			0.70	37.0			0.66	34.4
Stage 2	103	2.46			110	2.59			50	2.58		
			0.79	32.1			0.86	33.2			0.82	31.8
Stage 3	130	3.25			113	3.45			50	3.40		
			1.07	32.9			1.16	33.6			1.03	30.3
Stage 4	104	4.32			110	4.61			50	4.43		

land areas, and although the percentage growth per moult is consistently lower, the difference is small and of doubtful significance.

In order to obtain figures directly comparable with those given by Herrick and Hadley, an attempt was made to measure the total lengths of the Northumberland Strait larvae. Except for the 4th-stage larvae, however, reliable total length measurements could not be obtained because of difficulties in straightening the formalin-preserved specimens. The 50 4th-stage larvae averaged 14.4 mm. total length measured at a magnification of 12.4 from the tip of the rostrum to the posterior margin of the telson, exclusive of fringe. This figure is considerably higher than the averages of 12.6 mm. and 13.5 mm. presented by Herrick and Hadley but corresponds closely to the combined average of 14.6 mm. calculated by Templeman for Bay of Islands and Notre Dame Bay larvae.

The figures on percentage growth in carapace length per moult shown in Table III are much higher than those given by Herrick and Hadley based on total length. These differences result in part from a faster growth of the carapace as compared to total length, the carapace averaging 25.6 per cent of the total length in stage 1 (Templeman, 1948b), 30.8 per cent in stage 4 (4.43 mm.: 14.4 mm.) and 33 per cent or over in lobsters above 15 cm. total length (calculated from Table XIV). Templeman's figure of 25.6 per cent for the carapace length of 1st-stage larvae indicates that Northumberland Strait larvae in the 1st stage would average 7.5 mm. in total length. From stage 1 to stage 4, therefore, these larvae grow 6.9 mm. (92 per cent) in total length, whereas those reared by Herrick and Hadley grew 4.8 mm. (61 per cent) and 5.3 mm. (65 per cent), respectively.

On the basis of the data presented, it is concluded that larvae in nature grow considerably more per moult than those that have been reared under artificial conditions.

GROWTH OF 6- TO 10-INCH LOBSTERS UNDER NATURAL CONDITIONS

In order to find a method of marking lobsters that would permit selected size groups to be recognized after moulting, preliminary experiments were conducted at the Prince Edward Island Biological Station, Ellerslie, P.E.I., during

the summer of 1946. Five 7- to 8-inch (18–20 cm.) lobsters were marked on July 10 by cutting holes through the tail fan with a leather punch. Four of these died before moulting but the punch marks of one which moulted September 18 were clear enough to be encouraging.

During June 1947, three further experiments were started. In one, marked lobsters were held in concrete tanks at the Atlantic Biological Station, St. Andrews, N.B., to provide further information on the post-moult appearance of the marks. In the other experiments, designed to measure the growth of lobsters under natural conditions, lobsters were marked and liberated on the fishing grounds off southern Grand Manan, N.B., and Tignish, Prince Co., P.E.I.

This method of marking lobsters was introduced in Norway in 1899 by Appellof (1909) and later used on a larger scale by Dannevig (1936) in his growth studies. This earlier work was not brought to the writer's attention until 1948.

St. Andrews Marking Experiment

On June 27, 1947, 69 lobsters ranging from 8 to 10 inches (20–25 cm.) total length, which had been caught off southern Grand Manan on June 24, were transported to St. Andrews, where they were placed in indoor concrete tanks supplied with running sea water. Three of these were marked June 25 by means of a 3/16 inch (5-mm.) hole punched through one of the sections of the tail fan and the remainder marked June 29 and 30. To these were added eight lobsters of southern Nova Scotia origin which were purchased locally on March 13, 1947.

The lobsters were examined and fed fresh herring or flounders about twice each week until January 9, 1948, when the experiment was terminated, most of the lobsters having died prior to this date. Of the 77 lobsters, seven died from June 30 to July 30 before moulting and six others disappeared during the course of the experiment, apparently eaten by other lobsters either before or after moulting. All of the remaining 64 moulted once or twice.

Moulting started June 27, somewhat earlier than anticipated for this area of low summer temperatures, and occurred in two phases, 13 lobsters moulting between June 27 and August 7, the remainder going through the first moult between September 5 and November 25. The number of lobsters moulting each month and the average tank temperatures during the period of observation were as follows:

	No. moulting, first moult	*No. moulting, second moult*	*Average tank temperature*
			°C.
June 27–30	2		12.3
July	9		14.0
August	2		15.1
September	12		14.5
October	29	1	12.5
November	10	2	9.5
December	0	1	5.5
January 1–8	0	1	4.2
	64	5	

No appreciable difference in the growth of male and female lobsters occurred, as shown by the following average carapace lengths based on 60 lobsters which survived long enough after moulting to attain their full length.

	Number	*Average carapace length before moulting*	*Average carapace length after moulting*	*Growth*	
		mm.	*mm.*	*mm.*	*%*
Males	26	78.9	86.4	7.5	9.5
Females	34	76.5	84.0	7.5	9.8

Since it has been generally accepted that moulting is largely restricted to the summer and early fall and that except in warm, shallow areas lobsters of this size moult only once a year, the five Grand Manan lobsters which moulted twice are of particular interest. Their moulting and growth record was as follows:

		First Moult				Second Moult			
Sex	Carapace length	Date	Carapace length	Growth		Date	Carapace length	Growth	
	mm.		*mm.*	*mm.*	*%*		*mm.*	*mm.*	*%*
♀	76.9	June 27/47	83.0	6.1	7.9	Nov. 28/47	87.3	4.3	5.2
♀	71.5	June 28/47	78.5	7.0	9.8	Oct. 27/47	died	—	—
♀	83.4	July 4/47	92.0	8.6	10.3	Jan. 8/48	98.5	6.5	7.1
♀	73.5	July 12/47	79.4	5.9	8.0	Nov. 13/47	85.0	5.6	7.1
♂	71.1	July 13/47	76.9	5.8	8.2	Dec. 4/47	79.0	2.1	2.7

In each case growth following the second moult was less than that following the first, a result that probably should be anticipated in view of the demonstrated effect of holding on growth (Templeman, 1936a). In spite of the fact that tank temperatures from July to September exceeded bottom temperatures in this general area by 2° to 5°C. the experiment indicates that some 8- to 10-inch (20–25 cm.) lobsters off Grand Manan moult twice during a year and that some moulting can be expected during those months in which the average water temperature exceeds 4°C.

When the punch marks were examined after the moult, it was found that approximately 65 per cent could readily be recognized as such. Some marks, possibly those not originally clean cut, tended to grow in, and with other lobsters the section of the tail fan broke off at the marking point. Obliteration of the marks through mutilation by other lobsters occurred frequently enough under the crowded holding conditions to indicate that a considerably higher proportion of the marks would be recognizable under natural conditions. The five lobsters that moulted twice were equally recognizable after each moult.

Grand Manan and Tignish Marking Experiments, 1947-48

In the Grand Manan experiment, a total of 2,285 lobsters from 8 to 10 inches (20–25 cm.) total length were sexed, sorted into five carefully measured 1/8-inch (3.2–mm.) carapace-length groups and marked by means of a 3/16-inch (5–mm.)

diameter hole punched through one of the sections of the tail fan, each of the five tail fan sections representing one of the size groups. These lobsters were liberated on the fishing grounds in Seal Cove Sound from June 10 to 24, 1947, late enough in the year to prevent extensive recapture during the current legal fishing season which closed June 24, but early enough, it was thought, to avoid marking lobsters which had already moulted that year. Whenever possible lobsters were marked and liberated the same day they were caught, but on a few occasions it was necessary to hold marked lobsters in floating cars for periods up to 48 hours. In these and subsequent experiments, when selecting lobsters for marking, those seriously injured during fishing operations were avoided, since such mutilations would occur more frequently than in nature. When Emmel (1906), starting with 4th-stage larvae, repeatedly mutilated them by removing both chelipeds after each moult, their average length at the end of 4½ months was about 10 per cent less than non-mutilated controls.

Five of these marked lobsters were recovered from November 4 to 13, 1947, during special pre-season fishing conducted for tagging purposes. Examination of fishermen's catches by Fisheries Research Board personnel was started November 15, 1947, about five months after marking, and continued throughout the following winter (November 15, 1947, to January 15, 1948) and spring (May 1, 1948, to June 24, 1948) legal fishing seasons. From November 4, 1947, to June 24, 1948, a total of 178 marked lobsters were recovered. The carapace lengths of these as recorded in Table IV (Appendix) were measured to 1/32 inch with brass calipers especially designed and graduated for lobster carapace measurements.

Off Tignish the lobsters are considerably smaller, and a lower minimum-size limit is in effect. The marking experiment conducted here differed from the one at Grand Manan in that 6- to 8-inch (15–20 cm.) lobsters were marked. In these and subsequent experiments several factors were considered in selecting the size range to be marked. In order to evaluate present minimum size limits, it was considered important to obtain the best possible growth data for a range of lobsters centred around these limits. Since lobsters below present size limits cannot be sold legally, large numbers can be obtained from commercial fishermen at little expense. However, lobsters more than one inch (total length) below legal size are not usually caught in large quantities, particularly since the general adoption of minimum lath-space regulations. Even if readily available for marking, only the faster growing of these smaller sub-legal lobsters could be expected to attain legal size during one growing period, and these would provide biased growth estimates when subsequently recovered from fishermen's commercial landings. The marking of large legal-sized lobsters was limited principally by the high cost per individual lobster, but also by the general scarcity of these sizes.

Of the 2,446 marked lobsters liberated off Tignish during June 1947, only 56 were recovered during the 1948 spring season. The carapace lengths of these are listed in Table VI (Appendix).

Other Marking Experiments

The results of the 1947 marking experiments were encouraging enough to stimulate other marking experiments to determine the natural growth rates in other areas and to check the results already obtained. During the spring of 1948, marked lobsters were liberated off Port Maitland and Abbott's Harbour in southern Nova Scotia and off L'Archeveque, on the outer coast of Cape Breton, N.S. In the spring of 1950, marked lobsters were again liberated off Grand Manan, N.B., and off Tignish, P.E.I. The former experiment was to compare growth in 1950 with that in 1947, which was a year of unusually high water temperatures (Hachey and McLellan, 1947); the latter experiment to obtain a more reliable growth estimate for the Tignish area, since only 56 marked lobsters were recovered from the 1947 experiment. Marked lobsters were also liberated off Lismore, Pictou Co., N.S., during the spring of 1950 to obtain growth data for the Northumberland Strait area, which becomes relatively warm during summer.

In each of the 1950 experiments, the size range was extended by the addition of another ⅛-inch (3.2–mm.) carapace-length group. Some difficulty was experienced with the 1947 and 1948 experiments in deciding whether or not certain lobsters, particularly the smaller individuals, had been marked. This was overcome to a considerable extent in 1950 by marking two sections of the tail fan of each lobster, the six carapace-length groups being distinguished by different combinations of marks. Some indication of the variation in the post-moult appearance of these marks may be obtained from the photographs reproduced in Figure 3.

Marking experiments conducted to date are listed in Table XII together with pertinent information on minimum size limits and legal fishing seasons. The location of each of the experimental areas is shown in Figure 4. Detailed data on the number and sizes of lobsters marked and recovered in the 1948 and 1950 experiments are given in Tables V, VII, VIII, IX, X and XI (Appendix). The data for Lismore and the combined data for the two Grand Manan experiments are shown graphically in Figure 5.

Results

It will be noted in Tables IV to XI (Appendix) that some of the marked lobsters recovered fell in the same size range as when marked. Judging from their size and the appearance of the punch marks which were usually irregular and brown around the margin in contrast to the smooth, white scar tissue bordering the marks of moulted lobsters, it was concluded that these lobsters had not moulted. In these experiments, which involved the sorting of large numbers of lobsters into narrow size groups, some inconsistencies in measurement have undoubtedly occurred. The fact, however, that in only one case did the size reported at recapture fall below the size range of the particular group when marked indicates that errors in measurement have no serious effect on the results. The total number of marked lobsters recovered in each experiment and the number and percentage of these judged to have moulted were as follows:

	Total recovered	*Number moulted*	*Percentage moulted*
Grand Manan 1947	178	165	92.7
Grand Manan 1950	647	622	96.1
Tignish 1947	56	54	96.4
Tignish 1950	337	333	98.8
Abbott's Harbour 1948	230	229	99.6
Port Maitland 1948	145	121	83.5
L'Archeveque 1948	193	178	92.2
Lismore 1950	633	629	99.4
Totals	2419	2331	96.4

In all of the experiments, a total of 88 lobsters were classified as "non-moulters" and of these 71 (81 per cent) were distributed among the three larger groups marked. Less frequent moulting is to be expected among larger lobsters, particularly among mature females which do not moult during the periods in which external eggs are carried. In Canadian waters these egg-bearing periods usually last 11½ to 12 months (Templeman, 1940). Comparison of moulting frequency between size groups is, however, complicated by the fact that any sub-legal lobsters in the smaller size groups which failed to moult would not be landed for examination in proportion to their abundance.

Some mature females as small as 18 cm. have been found in the Tignish and Lismore areas. Although some of the larger lobsters marked at these ports were therefore undoubtedly mature, this appears to have had little effect on the moulting frequency, about 99 per cent of those recovered having moulted.

At L'Archeveque, where 18-cm. mature females have also been found, a larger minimum-size limit is in effect and larger lobsters were marked. A relatively high proportion of those marked were therefore mature, which probably accounts for the "non-moulters" which constituted 8 per cent of the recoveries. It might be expected from this argument that the majority of the "non-moulters" recovered at L'Archeveque would be female lobsters. Actually 13 of the 15 "non-moulters" recovered were males. Of the mature females marked in the spring of 1948, many of those which failed to moult during the summer of 1948 would lay eggs that same summer. Most of these would still be egg-bearing when commercial landings were examined for marked lobsters during the spring of 1949. Since egg-bearing females are protected by a regulation which is rigidly adhered to at L'Archeveque, egg-bearing "non-moulters" would not appear in the fishermen's landings. This suggests that the actual proportion which fail to moult may be considerably higher than the 8 per cent recorded in this experiment. This suggestion is supported by tag returns from this particular area.

Each year at L'Archeveque from 1945 to 1951 during the early part of the legal fishing season (May 20 to July 15), from 500 to 1,000 lobsters ranging from 22 to 35 cm. total length have been tagged with external tags which are lost on moulting. Recaptures during the spring season following the season in which the tagged lobsters were liberated indicate failure to moult. Since the number of recaptures made 12 to 14 months after tagging and the average percentage recapture during the tagging seasons are known, it is possible to estimate the total

TABLE XII. Summary of marking experiments.

Area	Marking			Recovery		Av. time between marking and recovery	Minimum size limit	Legal fishing season
	Period	Number	Approx. total length	Period	Number			
			cm.			*days*	*inches*	
Seal Cove Sound, Grand Manan, N.B.	June 10–24/47	2285	20–25	Nov. 4/47 to June 24/48	178	170	$3\frac{1}{4}^{a}$	Nov. 15 to Jan. 15 and May 1 to June 24
Tignish, P.E.I.	June 13–30/47	2446	15–20	May and June 1948	56	340	7^{b}	May 1 to June 30
Port Maitland, Yarmouth Co., N.S.	Apr. 19 to May 31/48	2901	20–25	Nov. 4/48 to May 13/49	145	223	$3\frac{1}{8}^{c}$	Dec. 1 to May 31
Abbott's Hbr., Yarmouth Co., N.S.	Apr. 26 to May 28/48	3746	20–25	Dec. 1/48 to Apr. 26/49	230	219	$3\frac{1}{8}^{c}$	Dec. 1 to May 31
L'Archeveque, Richmond Co., N.S.	June 2 to July 10/48	3431	20–25	May 21 to July 15/49	193	354	$3\frac{1}{8}^{c}$	May 20 to July 15
Seal Cove Sound, Grand Manan, N.B.	May 23 to June 22/50	2757	20–26	Nov. 3/50 to May 30/51	647	178	$3\frac{1}{4}^{a}$	Nov. 15 to Jan. 15 and May 1 to June 24
Tignish, P.E.I.	June 7–30/50	3502	15–21	May 5 to June 27/51	337	334	7^{b}	May 1 to June 30
Lismore, Pictou Co., N.S.	June 7–30/50	6262	15–21	May 5 to July 2/51	633	335	7^{b}	May 1 to June 30
Totals		27,330			2419			

[a] $3\frac{1}{4}$ inches (82.5 mm.) carapace length is equivalent to 9.4 inches (239 mm.) total length.
[b] 7 inches (177.8 mm.) total length is equivalent to 2.4 inches (61 mm.) carapace length.
[c] $3\frac{1}{8}$ inches (79.4 mm.) carapace length is equivalent to 9.0 inches (229 mm.) total length.

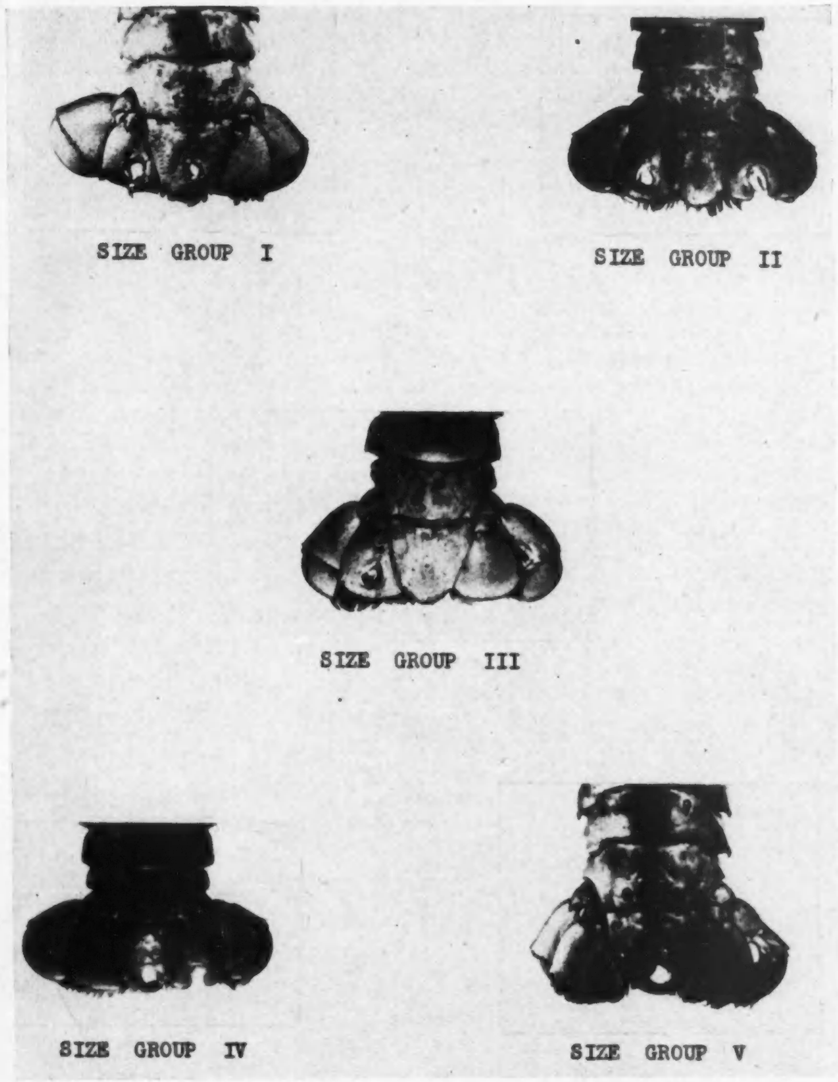

FIGURE 3. Photographs showing the post-moult appearance of marked lobsters and the combinations of marks used in the 1950 experiments to distinguish size groups. Lobsters marked at Lismore, N.S., June 1950, recovered May and June 1951. Size group VI not illustrated.

number of lobsters which carried tags at least 12 to 14 months. This figure related to the number which escaped the fishery during the tagging seasons provides an estimate of the percentage that failed to moult. In the following calculations the sexes are considered separately, and in order to have the results more directly comparable with the marking experiments, lobsters above 25 cm. have been omitted.

	Number of 22 to 25 cm. lobsters tagged 1945–1951	*Number and % recaptured during tagging season*	*Escapement*	*Number recaptured 12 to 14 months later*	*Estimated number retaining tags for 12 to 14 months*	*Percentage which failed to moult*
Males	1,295	802(61.9%)	493	71	115	23.3
Females	1,402	923(65.8%)	479	101	153	31.9

These tagging data indicate that of the sizes considered (22 to 25 cm.), about 23 per cent of the males and 32 per cent of the females failed to moult, estimates considerably higher than those suggested by the marking experiments for slightly smaller (20- to 25-cm.) lobsters. The retention of tags by fishermen from one season to the next would, of course, increase such estimates, but there is no evidence to indicate that this occurs to any serious extent in the L'Archeveque area.

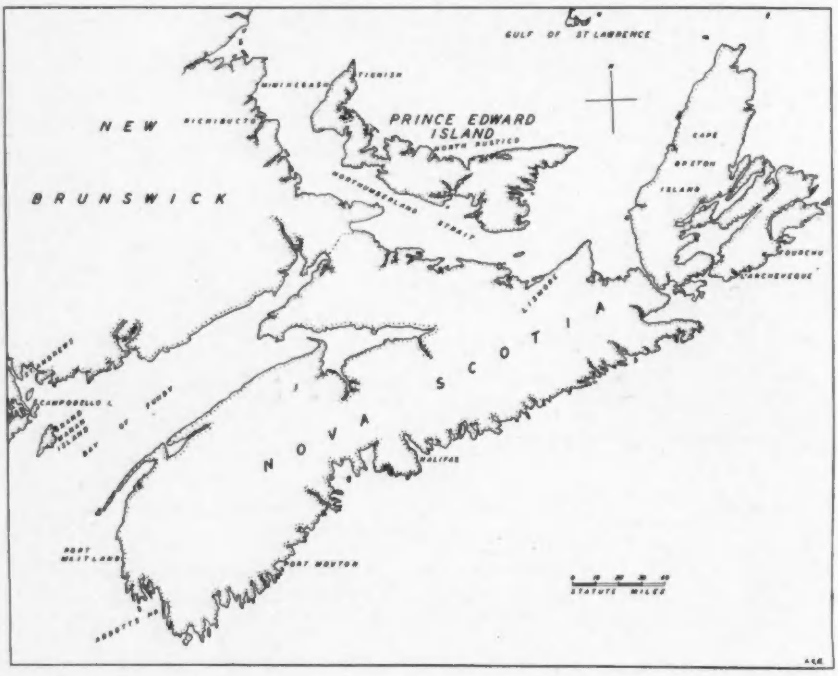

FIGURE 4. Outline map showing areas where marking experiments were conducted.

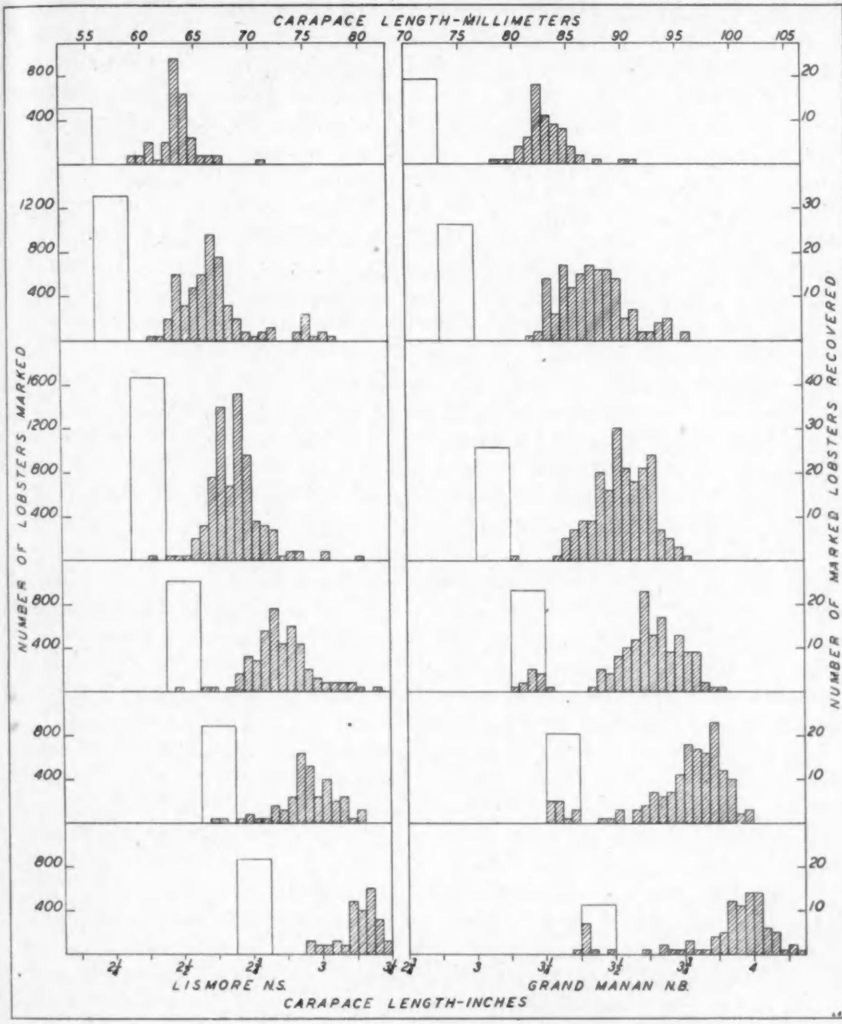

FIGURE 5. Size frequency distribution of lobsters marked (blank rectangles) and recovered (hatched rectangles) at Lismore, N.S., and at Grand Manan, N.B. Lismore lobsters marked June 7 to 30, 1950, recovered May 5 to July 2, 1951. Grand Manan lobsters marked June 10 to 24, 1947, and May 23 to June 22, 1950, recovered November 4, 1947, to June 24, 1948, and November 3, 1950, to May 30, 1951.

It is of interest to note that many of the female lobsters recaptured 12 to 14 months after tagging were reported by the fishermen as egg-bearing.

Off Grand Manan and southern Nova Scotia, the minimum size at

maturity is much larger than in the Gulf of St. Lawrence, the smallest egg-bearing females found in the course of this investigation at Grand Manan being 28 cm., at Port Maitland 31 cm., and at Abbott's Harbour 24 cm. At Grand Manan and Abbott's Harbour, the minimum size for mature lobsters may be even larger, since egg-bearing females which originated elsewhere are often released from holding units at these ports. It is concluded, therefore, that practically all of the lobsters marked at these three ports were immature. These lobsters were free on the average for only six months at Grand Manan and about seven months at Abbott's Harbour and Port Maitland. In these three areas, average bottom-water temperatures exceeding 4°C. occur from May to January (see data for station 5, Figure 8). Limited moulting could, therefore, as indicated by the St. Andrews marking experiment, be expected to occur as early as May and as late as January. It is concluded from this that if the lobsters marked at these ports had been free for a full year, virtually 100 per cent would have moulted.

On the basis of the above reasoning, "non-moulters" have not been included when calculating the annual average growth per size group. This procedure appears to be justified except at L'Archeveque where, because appreciable numbers of the mature lobsters marked apparently fail to moult, the growth estimate so calculated may be as much as 25 per cent too high.

From the size distributions given in Tables IV-XI (Appendix) the average carapace lengths of the moulted lobsters recovered in each group were calculated and converted to millimetres. These are listed in Table XIII together with the average sizes of the groups when marked and the average growth per group. Since no significant difference in growth could be detected in the two experiments conducted at Tignish, these data have been combined, as have those obtained from the two Grand Manan experiments.

Within each experiment, carapace growth is relatively constant throughout the size groups marked. Only in the L'Archeveque and Port Maitland data is there a suggestion that the larger lobsters grew more, and in these experiments relatively few lobsters were recoverd, particularly in the smallest and largest groups marked.

Although the weighted over-all average growth of the males exceeded that of the females in four of the five areas studied, the difference is small, averaging only 0.5 mm. for all experiments.

In order to estimate growth in total length and weight, series of carapace length, total length and weight measurements were made at Tignish, P.E.I., Lismore, N.S., Fourchu, N.S., and Port Mouton, N.S. Although Templeman (1935, 1944b) has shown considerable geographic variation in body form and weight–length relationship, it is believed that the Port Mouton measurements can be applied to the Grand Manan, Abbott's Harbour, and Port Maitland data without serious error. The Fourchu measurements have been applied to the L'Archeveque data, since these two fishing areas are contiguous. From these measurements, the straight-line equations listed in Table XIV were calculated. These equations were then used to estimate for each experiment the average total length and weight of the lobsters marked and recovered in each size group.

TABLE XIII. Size-group mid-points of lobsters marked; number, average carapace length and average growth of those recovered. All measurements in millimetres.

Size-group mid-point	Tignish, P.E.I., marked 1947 and 1950. Recovered 1948 and 1951.						Lismore, N.S., marked 1950. Recovered 1951.					
	Males			Females			Males			Females		
	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.
54.0	5	62.2	8.2	9	61.7	7.7	23	63.3	9.3	45	63.4	9.4
57.2	54	65.0	7.8	77	65.0	7.8	33	66.4	9.2	100	66.8	9.6
60.3	67	68.3	8.0	59	67.9	7.6	63	69.1	8.8	118	68.0	7.7
63.5	27	72.7	9.2	32	72.1	8.6	37	72.6	9.1	73	72.6	9.1
66.7	15	75.5	8.8	21	76.4	9.7	32	75.2	8.5	46	75.0	8.3
69.9	12	79.6	9.7	9	78.9	9.0	19	80.3	10.4	40	79.2	9.3
Tot. and Av.	180		8.4	207		8.1	207		9.1	422		8.8

Size-group mid-point	L'Archeveque, N.S., marked 1948. Recovered 1949.						Abbott's Harbour, N.S., marked 1948. Recovered 1948–49.					
	Males			Females			Males			Females		
	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.
71.5	3	80.8	9.3	3	79.8	8.3	10	83.4	11.9	20	82.2	11.1
74.6	26	83.7	9.1	19	84.0	9.4	27	86.2	11.6	41	85.4	10.8
77.8	38	88.6	10.8	28	87.9	10.1	40	89.9	12.1	31	90.1	12.3
81.0	18	92.6	11.6	15	91.2	10.2	25	92.4	11.4	15	91.8	10.8
84.2	19	99.3	15.1	9	96.2	12.0	12	95.9	11.7	8	95.8	11.6
Tot. and Av.	104		11.3	74		10.0	114		11.7	115		11.3

Size-group mid-point	Port Maitland, N.S., marked 1948. Recovered 1948–49.						Grand Manan, N.B., marked 1947 and 1950. Recovered 1947–48 and 1950–51.					
	Males			Females			Males			Females		
	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.	No.	CL.	Inc.
71.5	8	80.9	9.4	6	80.4	8.9	23	83.5	12.0	45	83.0	11.5
74.6	15	82.0	7.4	16	84.7	10.1	74	87.7	13.1	83	86.9	12.3
77.8	24	87.9	10.1	16	87.6	9.8	96	90.1	12.3	101	89.5	11.7
81.0	15	93.4	12.4	10	92.4	11.4	71	92.9	11.9	66	92.2	11.2
84.2	5	94.7	10.5	6	95.8	11.6	79	95.9	11.7	64	96.4	12.2
87.3							43	100.3	13.0	42	100.6	13.3
Tot. and Av.	67		10.0	54		10.2	386		12.3	401		11.9

Over-all averages, weighted according to the number of lobsters recovered in each size group, were then calculated for each experiment and are shown in Table XV.

From these data, it is concluded that in the southern Gulf of St. Lawrence the annual growth of 15- to 20-cm. lobsters (some mature) is 8 to 9 mm. (13 to 15 per cent) in carapace length, 22 to 25 mm. (13 to 14 per cent) in total

Table XIVa. Equations relating carapace length (CL) and total length (TL). Measurements in millimetres.

Port	Males			Females		
	No.	Range of CL.	Equations	No.	Range of CL.	Equations
Tignish, P.E.I.	196	53–116	$CL = 0.3735 \; TL - 4.53$	215	51–106	$CL = 0.3480 \; TL - 1.38$
Lismore, N.S.	44	59– 94	$CL = 0.3750 \; TL - 4.88$	47	57– 95	$CL = 0.3481 \; TL - 1.31$
Fourchu, N.S.	71	61–110	$CL = 0.3954 \; TL - 8.68$	70	61–105	$CL = 0.3618 \; TL - 3.77$
Port Mcuton, N.S.	138	56–133	$CL = 0.3744 \; TL - 5.73$	127	56–114	$CL = 0.3531 \; TL - 2.58$

Table XIVb. Equations relating weight (W) and carapace length (CL). Weights in grams, lengths in millimetres.

Port	Males			Females		
	No.	Range of CL.	Equations	No.	Range of CL.	Equations
Tignish, P.E.I.	147	53–116	$\log W = 3.2068 \; \log CL - 3.4806$	171	51–106	$\log W = 2.9456 \; \log CL - 2.9977$
Lismore, N.S.	44	59– 94	$\log W = 3.1063 \; \log CL - 3.3116$	47	59– 94	$\log W = 2.8965 \; \log CL - 2.9156$
Fourchu, N.S.	66	61–109	$\log W = 3.1400 \; \log CL - 3.3678$	70	61–105	$\log W = 2.8743 \; \log CL - 2.8573$
Port Mouton, N.S.	162	77–127	$\log W = 3.0218 \; \log CL - 3.1364$	169	75–136	$\log W = 2.8435 \; \log CL - 2.7849$

TABLE XV. Over-all average carapace lengths (CL), total lengths (TL) and weights (W) of lobsters when marked and recovered. Total lengths and weights were determined for each size group from appropriate equations in Table XIV, then weighted in proportion to number recovered to give over-all average. Lengths in millimetres, weights in grams.

Port	Marked						Recovered						Growth						Percentage growth					
	CL		TL		W		CL		TL		W		CL		TL		W		CL		TL		W	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Tignish, P.E.I.	60.8	60.4	175	178	176	179	69.2	68.5	197	201	266	260	8.4	8.1	22	23	90	81	13.8	13.4	12.6	12.9	51.1	45.2
Lismore, N.S.	61.5	61.0	177	179	179	183	70.6	69.8	201	204	274	270	9.1	8.8	24	25	95	87	14.8	14.4	13.6	14.0	53.1	47.5
L'Archeveque, N.S.	78.5	78.2	221	226	385	385	89.8	88.2	249	254	590	546	11.3	10.0	28	28	205	161	14.4	12.8	12.7	12.4	53.2	41.8
Abbott's Harbour, N.S.	77.9	76.4	223	224	381	374	89.6	87.7	255	256	584	554	11.7	11.3	32	32	203	180	15.0	14.8	14.4	14.3	53.3	48.1
Port Maitland, N.S.	77.5	77.5	222	227	376	388	87.5	87.7	249	256	544	554	10.0	10.2	27	29	168	166	12.9	13.2	12.2	12.8	44.7	42.8
Grand Manan, N.B.	79.8	79.0	228	231	412	412	92.1	90.9	261	265	634	614	12.3	11.9	33	34	222	202	15.4	15.1	14.5	14.7	53.9	49.0

length and 80 to 95 grams (45 to 53 per cent) in weight. The slightly faster growth at Lismore as compared to Tignish is associated with somewhat higher summer temperatures at Lismore. The bi-modal distribution of the Lismore group-II (Figure 5) recoveries indicates that some of these lobsters moulted twice.

In southern Nova Scotia and Grand Manan, 20- to 25-cm. immature lobsters grow somewhat faster, the carapace increasing 10 to 12 mm. (13 to 15 per cent), total length 27 to 34 mm. (12 to 15 per cent) and weight 170 to 220 grams (43 to 54 per cent).

As discussed previously, a high proportion of the 20- to 25-cm. lobsters marked at L'Archeveque were mature. Since there is evidence that in this area appreciable numbers of this size do not moult every year, the L'Archeveque growth estimates are probably too high.

Comparison with Previous Growth Estimates

Herrick (1896) recorded the moults of eight 5½- to 11¼-inch (14 to 28.6 cm.) lobsters. The growth in total length varied from 1 to 1½-inches, or 6.7 to 18.2 per cent, averaging 12.0 per cent.

Hadley (1906) reasoned from very limited data that 18- to 27-cm. lobsters grew 11 per cent in total length at each moult. He reasoned further, largely on the basis of smaller lobsters reared in captivity in warm surface waters, that 18- to 22-cm. lobsters moulted twice a year.

Dannevig (1936), using the method described in this paper, marked 2,566 European lobsters (*H. vulgaris*) which he released along the Skagerak coast of Norway. Of these, 1,305 were recovered. The minimum sizes at maturity in this area and in the southern Gulf of St. Lawrence appear to be similar, Dannevig reporting mature males as small as 16 cm., and berried females down to 20 cm. at least. The average growth per year of the 17- to 20-cm. size group was 25 mm. for males and 22.5 mm. for females. This estimate corresponds closely to those obtained by the writer for the Tignish and Lismore areas in the southern Gulf of St. Lawrence.

Templeman (1936a) showed that 14- to 20-cm. lobsters caught in the Point du Chêne, N.B., area of Northumberland Strait and held in crates for several days before moulting grew 12 to 13 per cent in one moult, the males growing slightly faster. He argued on the basis of shell-condition studies, that in such high summer-temperature areas as Malpeque Bay, P.E.I., the lagoons of the Magdalen Islands, and western Northumberland Strait, lobsters up to 23 cm. in length moult twice a year, the first moult occurring in June and July, the second in late summer or early fall. In the same paper he presented data on the growth of 25- to 35-cm. Grand Manan lobsters which had been held in a pound for two to five months. Growth per moult in these lobsters averaged about 9 per cent.

Templeman (1948b) recorded the growth per moult of 10 male and six female Point du Chêne lobsters which moulted within one or two days of capture.

The males which varied from 51 to 70 mm. in carapace length (15 to 20 cm. total length) grew on the average 10.3 mm. (16.9 per cent) in carapace length, the maximum growth observed being 19.6 per cent. Growth of the 51- to 66-mm. females averaged 8.6 mm. (14.3 per cent), the maximum being 16.4 per cent.

These previous estimates of growth per moult agree fairly well with the writer's estimate of annual growth, Herrick's and Hadley's being somewhat less and Templeman's 1948 estimate being somewhat greater, particularly for male lobsters.

The maximum growth per moult recorded by Templeman was 19.6 per cent for a 16-cm. male and by Herrick 18.2 per cent for a 14-cm. female. The greatest growth per moult among the Grand Manan lobsters held at St. Andrews in 1947, under rather unfavourable conditions, was 19.5 per cent for a 22-cm. female. It would appear from these records that the maximum natural growth per moult for lobsters of this general size range would be of the order of 20 per cent for both sexes. Any recaptured marked lobsters which exceeded the maximum size of their group when marked by more than 20 per cent could be considered as having moulted twice. On this basis only 44 of the 2,419 lobsters recovered from all marking experiments would be classified as "double moulters", 23 of these being found at Lismore, 15 at Grand Manan, five at Tignish, and one at Abbott's Harbour. It is concluded from this, that in the areas studied, most of the lobsters within the size ranges marked moult only once a year. Only in the group-II Lismore and Grand Manan data is there an indication that more than a very few of the lobsters moulted twice.

In certain shallow areas in the southern Gulf of St. Lawrence such as Malpeque Bay, P.E.I., and the Point du Chêne area of Northumberland Strait where summer bottom water temperatures are unusually high, immature lobsters probably moult more frequently.

ESTIMATED GROWTH RATE OF LOBSTERS

The natural growth per moult of the first three larval stages is given in Table III. The annual growth of 15- to 25-cm. marked lobsters of unknown stages is summarized in Tables XIII and XV, and some evidence has been presented which indicates that in the majority of cases the annual growth of these marked lobsters represents a single moult. Rate of growth estimates involve, however, not only the growth per moult but also the frequency of moulting. Largely because of the difficulty in capturing the early bottom stages, few observations have been made on them in nature.

An attempt has, therefore, been made to estimate the natural growth per moult of these intermediate sizes from the data available. From the seasonal distribution of the first four larval stages, the local temperature records, and Templeman's experimental work on the effect of temperature (Templeman, 1936b, 1948b) an attempt has also been made to estimate the frequency of moulting.

Growth per Moult—Stages 1 to 20

When carapace lengths before moulting of both larvae and 15- to 25-cm. lobsters are plotted on a double logarthmic scale against the carapace length after moulting as in Figure 6 the points are seen to fall on a straight line. In

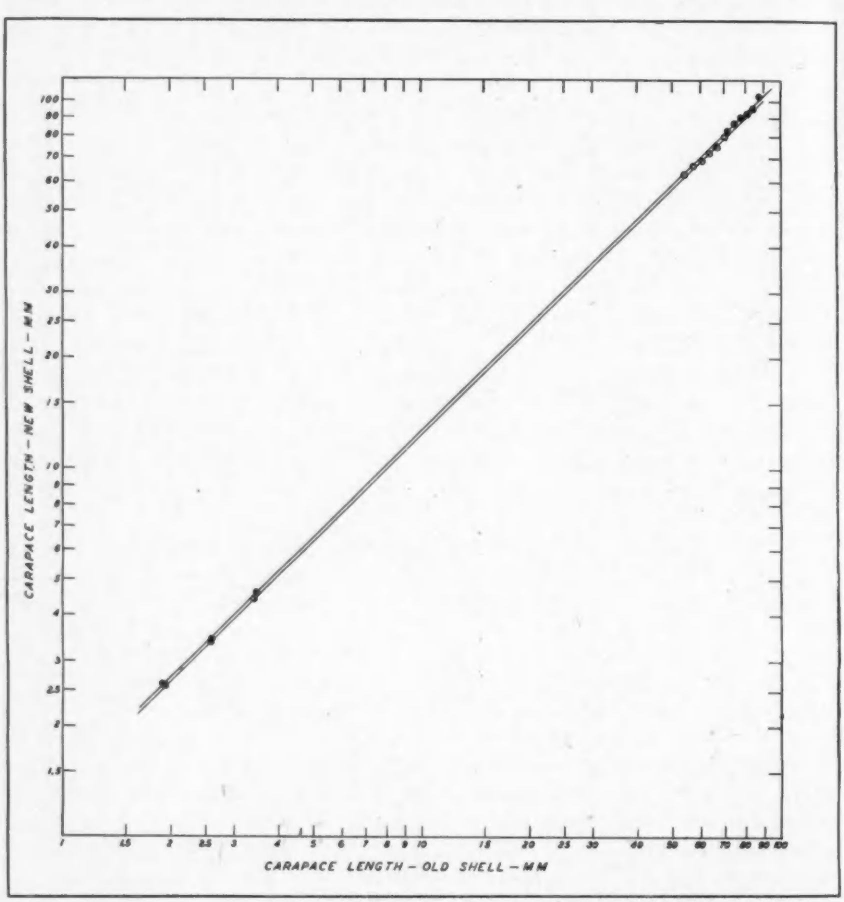

Figure 6. Logarithmic relation of carapace length before moulting to carapace length after moulting. Open circles represent larvae caught off Richibucto, N.B., and marked male lobsters recovered at Lismore, N.S. Closed circles represent larvae caught in Notre Dame Bay, Newfoundland (Templeman, 1948b) and marked male lobsters recovered at Grand Manan, N.B.

relating the growth of larvae and larger lobsters, Templeman's larval measurements from Notre Dame Bay on the east coast of Newfoundland have been used in conjunction with the marked lobsters recovered at Grand Manan. Presumably

conditions for growth in the relatively cool Notre Dame Bay area are more similar to Grand Manan than are those in the high summer-temperature area where the Richibucto larvae were captured. The following equations relating carapace length before moulting (X) and carapace length after moulting (Y) have been calculated by the method of least squares.

Grand Manan and Notre Dame Bay

Males: $\text{Log}\, Y = 0.9555 \log X + 0.1473$
Females: $\text{Log}\, Y = 0.9546 \log X + 0.1476$

Lismore and Richibucto (Northumberland Strait)

Males: $\text{Log}\, Y = 0.9555 \log X + 0.1394$
Females: $\text{Log}\, Y = 0.9545 \log X + 0.1400$

When the size of 4th-stage larvae is known and it is assumed that these equations describe the growth of subsequent stages, it is possible to calculate the average size of the lobsters at each stage up to the maximum sizes recovered in the marking experiments. These calculated carapace lengths are listed in Table XVI together with the corresponding total lengths. The total lengths of

TABLE XVI. Carapace lengths (mm.) and total lengths (mm.) of lobsters in stages 4 to 20. Carapace lengths are calculated from equations relating carapace length before moulting to carapace length after moulting. Total lengths (except stage 4) are calculated from appropriate carapace length–total length equations.

	Grand Manan, N.B.				Lismore, N.S.			
	Males		Females		Males		Females	
Stage	CL	TL	CL	TL	CL	TL	CL	TL
4	4.61	15.0	4.61	15.0	4.43	14.4	4.43	14.4
5	6.05	18	6.04	18	5.72	17	5.71	17
6	7.84	23	7.82	23	7.28	22	7.28	22
7	10.0	29	10.0	29	9.18	27	9.18	27
8	12.7	37	12.7	37	11.5	34	11.5	34
9	15.9	47	15.9	47	14.2	42	14.2	42
10	19.8	58	19.6	57	17.4	51	17.3	51
11	24.3	71	24.1	70	21.1	62	21.0	62
12	29.6	86	29.3	85	25.4	74	25.2	74
13	35.8	104	35.3	103	30.3	88	30.1	88
14	42.8	125	42.2	123	35.9	105	35.6	104
15	50.8	151	50.0	149	42.2	123	41.7	122
16	59.9	175	58.8	174	49.3	144	48.6	142
17	70.1	203	68.7	202	57.1	165	56.2	165
18	81.5	233	79.6	233	65.7	188	64.6	189
19	94.0	266	91.7	267	75.2	214	73.8	216
20	107.9	303	104.9	304	85.6	241	83.7	244

lobsters under 50 mm. in carapace length were calculated using the equation, $CL(\text{mm.}) = 0.344\ TL(\text{mm.}) - 0.13$. This equation was derived from measurements of 158 male and female lobsters ranging from 8 to 57 mm. in carapace length caught off Richibucto, N.B. Total lengths for lobsters above 50 mm. carapace length were calculated from the appropriate equations in Table XIV.

These calculations indicate that in the Northumberland Strait area lobsters attain a length of 19 cm. by the 18th stage. This figure is somewhat higher than Hadley's estimate of 14.1 cm. for this stage (Hadley, 1906), but considerably lower than Templeman's estimate of 25.8 cm., which was based on larvae caught in Newfoundland and on larger lobsters principally from the Point du Chêne area of Northumberland Strait (Templeman, 1948b).

The Grand Manan calculations, which suggest that in the Bay of Fundy area lobsters reach a length of 23 cm. by the 18th stage, are open to more serious question. In spite of considerable plankton towing in this general area over the past 35 years, only three lobster larvae have been captured, one 4th-stage (?) taken off Campobello Island August 17, 1936, one 2nd-stage caught off Bocabec, N.B., on August 6, 1951, and one 1st-stage caught off southern Grand Manan, N.B., August 14, 1952. The size and growth per moult of the larvae in this area may well be different from that reported by Templeman for Notre Dame Bay. If the Richibucto larvae are taken as representative of the Grand Manan area, the estimate for 18th-stage males is reduced to 21.3 cm.

Moulting Frequency and Age Estimates

Templeman (1936b) reared larvae through the first four stages at various temperatures from 6.7° to 23.8°C. The number of days spent in stage 4 at different temperatures has been estimated from his Figure 1 as follows:

Temp. °C.	10	11	12	13	14	15	16	17	18	19	20
Days	50	38	32	28	25	23	21	19	17	15	13

The same worker (Templeman, 1948b) presented data on the number of days spent in each of the stages from one to twelve at an average temperature of 19.7°C. These data which have been plotted in Figure 7 apparently follow a straight-line relationship of the form $Y = 2.856\,X - 0.13$, where Y represents the number of days and X the stage. The number of days spent in each stage as calculated from this equation are as follows:

Stage	1	2	3	4	5	6	7	8	9	10	11	12
Days	2.7	5.6	8.4	11.3	14.2	17.0	19.9	22.7	25.6	28.4	31.3	34.1
Days relative to stage 4				1.00	1.26	1.50	1.76	2.01	2.26	2.51	2.77	3.02

Assuming that the ratio of the time spent in stage 4 to the time spent in any subsequent stage is constant from 10° to 20°C., it is possible from the above data to estimate the length of the 5th- to 12th-stage periods at various temperatures.

Water temperatures taken at the surface and at 10 metres off North Rustico, P.E.I., and at Station no. 5 off Campobello Island, N.B., from 1945 to 1949 have been averaged by months and are plotted in Figure 8. The North Rustico data, which were provided through the courtesy of Dr. L. Lauzier from the files of the Atlantic Herring Investigation Committee, may be considered representative of the southern Gulf of St. Lawrence. The Station no. 5 data are typical of the Bay of Fundy area.

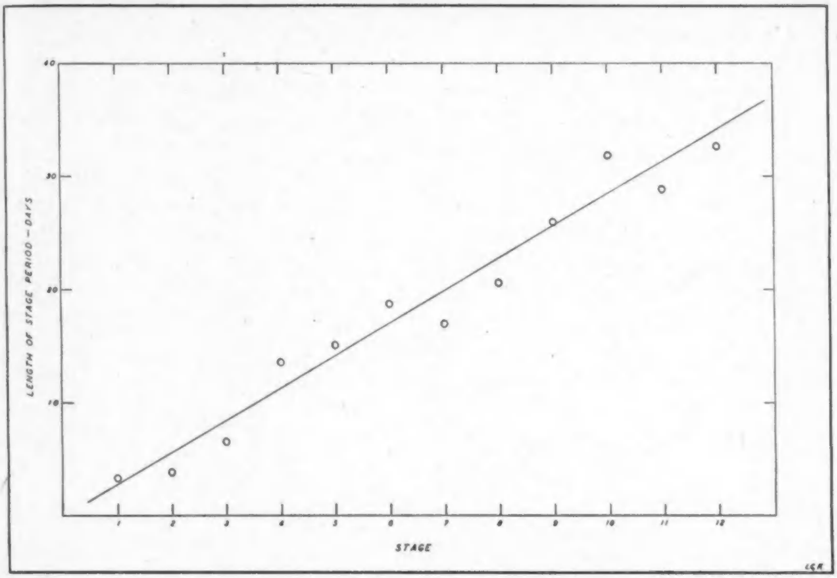

FIGURE 7. Number of days spent in stages 1 to 12 at 19° to 21°C. Data from Templeman (1948b).

The 1948 to 1952 tows for lobster larvae which are summarized in Table I show that in the Richibucto area 4th-stage larvae occur from about mid-July to late September. Some have been taken as early as July 12, presumably shortly after moulting into this stage. At an average surface temperature of 16.7°C. these should moult into the 5th stage about August 1. With August temperatures at 10 metres averaging 18.4°C., 5th-stage larvae at this depth should reach the 6th stage in about 20 days and be almost halfway through this stage by the first of September. At the September average of 15.3°C., the remainder of the 6th stage could be completed by September 17. About one-third of the 7th stage could be completed during the remainder of September, with the final moult for the season into the 8th stage taking place during early November.

Assuming that the last 4th-stage larvae caught (September 22) were more than halfway through this stage, they could be expected to reach the 5th stage by the first of October. At an average temperature of 11.9°C. most of the 5th stage should be completed during October and these larvae could be expected to moult into the 6th stage during November.

It would appear from this line of reasoning that in the Northumberland Strait area most lobsters moult only five to seven times during their first growing season and pass their first winter in the 6th, 7th and 8th stages.

At 12°C. 7th-stage lobsters are estimated to require 56 days to complete this stage. Those passing their first winter in the 7th stage in the Richibucto area

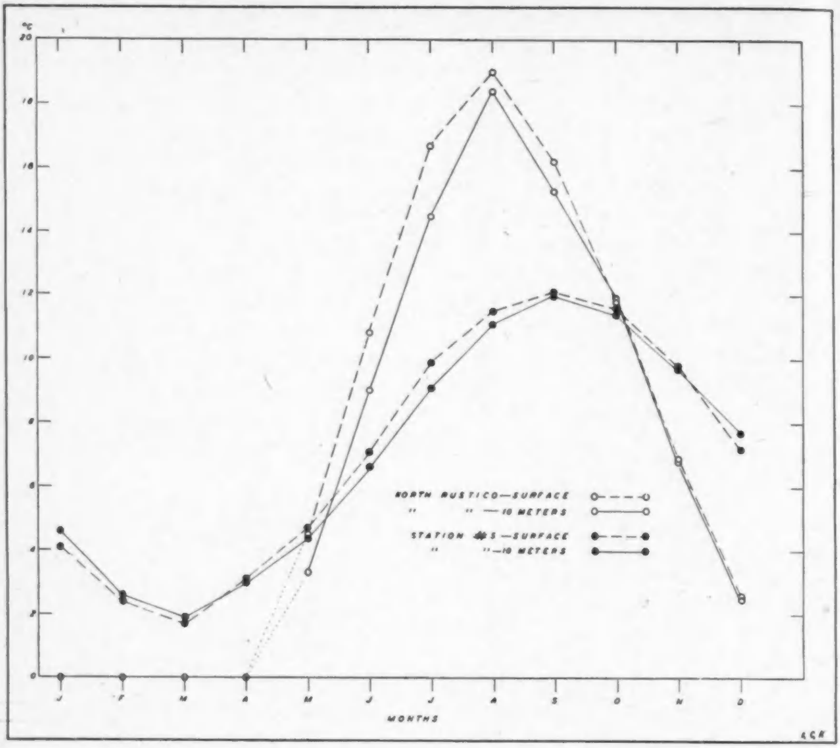

FIGURE 8. Average monthly water temperatures at the surface and 10 metres (5½ fathoms) off North Rustico, P.E.I., and Campobello, N.B.

could therefore reach the 8th stage towards the end of July. At 18.4°C. this stage could be completed during August, and only one more moult from the 9th to the 10th stage during the latter part of October would appear to be possible before the onset of winter.

If the same line of reasoning is followed, it would appear unlikely that lobsters would moult more than twice during their third, fourth and possibly fifth growing seasons. Thus it seems that in the Northumberland Strait area most lobsters would complete their fifth growing season in the 16th stage at an average length of 14 cm. (5½ in.). Their age, calculated from August 1, the approximate mid-point of the hatching period, would be about 4¼ years.

If, as indicated by the marking experiments, the majority of lobsters beyond the 16th stage moult only once a year, the 20th stage would not be reached until the lobster had completed nine growing seasons. At this stage the Northumberland Strait lobster is estimated to be 241 mm. (9½ in.) long and 8¼ years old.

These age estimates are considerably higher than those derived by Hadley for the American lobster (*H. americanus*), but agree closely with Dannevig's estimate for the European lobster (*H. vulgaris*). Hadley (1906) judged a 141-mm. lobster to be 2½ years old and a 247-mm. male 5 years. Hadley's estimate was based on the assumption that the percentage growth per moult remained constant (18 per cent) from stage 1 to 16, whereas the writer's observations indicate that the percentage growth per moult drops gradually from about 34 per cent at stage 1 to 16 per cent at stage 16. Hadley also differed from the writer regarding the frequency of moulting, reporting that the 12th stage was reached at the end of the first year. Hadley's conclusions regarding the frequency of moulting during the first three growing seasons were based on lobsters held at Wickford, Rhode Island, in shallow, floating troughs from spring until fall. The average monthly surface temperatures at Wickford from April to October 1905, calculated from chart IV given in the 36th Annual Report of the Rhode Island Commission of Inland Fisheries for 1905, were as follows:

Month	April	May	June	July	August	September	October
Temp. °C.	8.1	11.6	17.9	22.5	21.8	18.8	12.7

At these high surface temperatures the early bottom stages would moult more frequently than in nature.

Dannevig, who appears to have had the most extensive data on the growth of the European lobster, concluded (1936) that lobsters along the Skagerak coast of Norway attained a length of 21 cm. in about seven years. According to the writer's estimate, lobsters in the Northumberland Strait area reach a length of 21 cm. (19th stage) at the end of their 8th growing season when they are about 7¼ years old.

Templeman's calculations and those of the writer are in essential agreement regarding the frequency of moulting during the first growing season. They differ principally regarding the growth per moult during the early bottom stages, Templeman (1948b) concluding that the growth per moult declined from 33 per cent at stage 4 to 26 per cent at stage 10, the corresponding figures derived by the writer being 29 and 21 per cent respectively.

In the Bay of Fundy area where summer water temperatures are low, moulting during the larval stages, at least, is probably less frequent. The effect of these low summer temperatures on the moulting frequency of larger lobsters may, however, be partially counterbalanced by the relatively moderate winter temperatures. Among the sizes of lobsters marked, growth per moult was slightly greater in this area than in the southern Gulf of St. Lawrence. Furthermore, maturity, which reduces the growth per moult and the frequency of moulting, occurs at a much larger size in the Bay of Fundy. It appears, therefore, that although the growth rate in the Bay of Fundy area may be initially slower, it eventually exceeds the rate in the Gulf of St. Lawrence, where the minimum size at maturity is about 10 cm. less. In the present state of our knowledge regarding larval and early bottom stages in the Bay of Fundy, age estimations for this area appear to be rather futile.

LARVAL PLANTING EXPERIMENTS, SCHOODIC, MAINE

Taylor and Baird (1948) and Taylor (1949) have reported on the planting of 4th-stage larvae in a pound located at Schoodic Point, Maine. The larvae, which were artificially reared in heated water at the Boothbay Harbour, Maine, rearing station, presumably reached the 4th stage considerably sooner than they would have in nature. These larvae were stated to be about 0.47 inches (11.9 mm.) in length, considerably smaller than those measured by Templeman and the writer from nature. In 1947 two lots of larvae were planted, 8,701 on June 22 and 3,200 on July 17. An additional planting of 10,000 4th-stage larvae was made July 12, 1948.

The pound, a small cove enclosed by a 200 foot (61-m.) dam, was about 375 ft. (114 m.) long, 250 ft. (76 m.) wide at its widest point and had a maximum depth of 6 ft. (1.8 m.) at low tide. The two water temperatures reported, 11.7°C. on June 22, 1947, and 17.2°C. on July 17, 1947, indicate that bottom temperatures in this shallow, enclosed basin are considerably higher than along the open Maine coast.

The pound was drained and searched for small lobsters on November 15, 1947, June 7, 1948, and November 23, 1948. The 22 lobsters recovered November 15 varied from 25 to 54 mm. in total length, averaging 43.9 mm. Of the 56 recovered in the June 7 examination, all but one fell within the range 27 to 56 mm., the one exception measuring 102 mm. The over-all average length was 43.2 mm., indicating that no growth had occurred from November 15, 1947, to June 7, 1948. The 64 lobsters recaptured November 23, 1948, which varied from 25 to 135 mm., included specimens from both the 1947 plantings and the 1948 plantings. Taylor, assuming that those over 59 mm. were survivors of the 1947 plantings, calculated the average size of this age group as 77.3 mm.

According to the estimates for the Northumberland Strait area, lobsters ranging from 25 to 56 mm. would be in the 7th to 10th stage. Since the artificially reared 4th-stage larvae were considerably smaller than those found in nature, the Schoodic lobsters were possibly in the 8th to 11th stages when recaptured in November 1947, and June 1948. Considering the high temperatures to which these lobsters were exposed during rearing and after planting, somewhat more frequent moulting than that estimated for the first growing season in the Northumberland Strait area is not unexpected.

During their second growing season, the Schoodic lobsters grew from an average length of 43 mm. to an average of 77 mm., an increase of 34 mm. The Northumberland Strait estimates indicate that 41-mm. lobsters grow an additional 34 to 35 mm. in three moults, the number of moults calculated to occur in this area during the second growing season.

OBSERVATIONS ON SMALL LOBSTERS IN NATURE

Although the four free-swimming larval stages are readily caught in large numbers, the early bottom stages, in spite of persistent and varied attempts over many years, evaded capture until the autumn of 1952. From September 19 to October 27, a series of 208 mostly 10-minute bottom drags was made off Richi-

bucto, N.B., usually at 1 to 5 fathoms (1.8–9.2 m.) but including some to 12 fathoms (22 m.).

The bottom drag is shown in Figure 9. The drag frame, 3½ feet (1.1 m.) long,

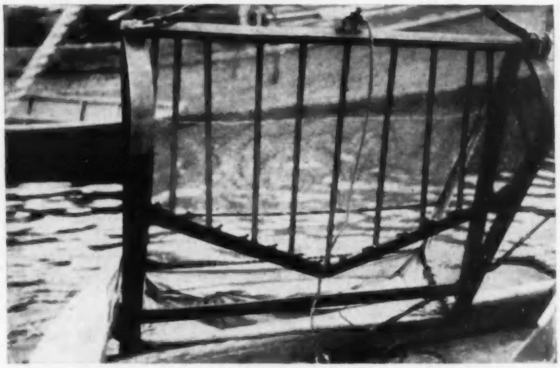

FIGURE 9. Drag frame standing on back end, viewed from below.

4½ feet (1.4 m.) wide and 1 foot (30 cm.) deep, consisted of two iron shoes, separated and supported by iron pipe and bars. A series of iron rods spaced 6 inches (15 cm.) apart ran obliquely from the top of the mouth to a v-shaped bar fastened to each shoe across the bottom of the frame. These rods served to keep large rocks out of the net. The iron teeth on this v-shaped bar furrowed the bottom to a depth of about one inch. The space behind the v-shaped bar was provided to get rid of much of the heavier debris. The sides and top of the frame were covered with ¼-inch (6-mm.) mesh galvanized wire. The net, 10 feet (3 m.) long, was made of woven nylon, 7 meshes to the inch and was protected from wear by a piece of canvas along the bottom.

In the 208 drags, a total of 432 lobsters ranging from 8 to 77 mm. carapace length (23 to 224 mm. total length) were caught. Of these, 91 were 4 inches (102 mm.) or less in total length. The size distributions of these and other lobsters in this range found previously are reported in the literature are listed in Table XVII.

The 19 Richibucto lobsters in the 25- and 30-mm. classes, all of which were captured during October on the following dates, 6th (1), 17th (4), 23rd (10), 24th (3), and 27th (1), are of particular interest. These lobsters, which varied from 8.0 to 11.0 mm. carapace length (av. 9.2) and from 23 to 31 mm. total length (av. 26.6), are distinctly separate from the next larger group and were without doubt hatched during the summer of 1952. At the time of capture, they presumably had virtually completed their first growing season. The moulting-frequency estimate indicates that in the Northumberland Strait area most of the lobsters pass their first winter in stages 6, 7 and 8, at calculated average total lengths of 22, 27 and 34 mm. The size range of these 19 lobsters agrees remarkably well with these calculated sizes.

The length-frequency distribution of this small sample gives no indication

Table XVII. Total length distributions of small lobsters found in nature. The class interval is 5 mm.

Vicinity	Dates	Method of capture	Class mid-point 25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Totals
Grand Manan, Charlotte Co., N.B.	Oct., 1947	Found in cod stomachs									1	1							2
Grand Manan, Charlotte Co., N.B.	May 21 to June 20, 1949	Lobster traps										2	1				1		4
L'Etang, Charlotte Co., N.B.	June 1, 1948	Found by diver								1									1
Bocabec, Charlotte Co., N.B.	July 20 to Aug. 16, 1938–1951	Found under rocks at low tide		1	1					1	1	1	2	2	0	4	2	1	16
Shediac, Westmorland Co., N.B.	Aug. 28, 1943	Lobster trap									1								1
Richibucto, Kent Co., N.B.	Sept. 19 to Oct. 27, 1952	Bottom drag	12	7	0	1	1	5	1	5	4	2	7	6	7	10	8	15	91
Malpeque Bay, P.E.I.[a]	July 3 to Aug. 11, 1919	Small lobster traps, beam trawl and dip nets									2	0	2	3	2	13	11	21	54
Malpeque Bay, P.E.I.[a]	July 17 to Aug. 20, 1920	Small lobster traps								1	2	5	16	7	6	21	11	18	87
Gad's Harbour Newfoundland[b]	June 30, 1938	Found under rocks at low tide														1			1
Gad's Harbour, Newfoundland[b]	Aug. 29, 1938	Found under rocks at low tide		1					1	1									3
Casco Bay, Maine[c]	Aug. 31 to Oct. 19, 1893	Found under rocks at low tide				1	1	1	1	2	2	4	4	1	5	1	4	3	30
Woods Hole, Mass.[c]	Jan. 28, 1882	Washed ashore in storm				3	0	3	2	1	1	0	2	1	2				15

[a] MacKay (1919, 1920). [b] Templeman (1945). [c] Herrick (1896).

of modes corresponding to particular stages, as might be anticipated from the discrete size ranges of the first four larval stages. Stage identification by this method may be possible when larger numbers of these early bottom stages are obtained.

Stage identification on the basis of morphological characters as described by Templeman (1948a) was attempted. Although positive identification of each lobster was not possible, some in the sample were identified as stages 6 and 7, with the remainder older, presumably in stage 8.

The three 30- to 35-mm. (av. 1¼-inch) lobsters found at Bocabec, N.B., and Gad's Harbour, Newfoundland, during July and August were almost certainly yearlings, which, according to Table XVI, would be in the 7th or 8th stage. This suggests that these lobsters passed their first winter in the 6th or 7th stage and had completed one more moult before capture. The three or four smallest lobsters (40 to 55 mm.) taken from August 31 to October 19 in Casco Bay were also in all probability yearlings which reached the 6th to 8th stage at the end of their first growing season and had completed two additional moults during the season in which they were captured. The 40-mm. lobsters found at Woods Hole in January were, no doubt, passing through their first winter, probably in the 8th or 9th stage. All of these rather limited observations provide support for the writer's conclusions regarding moulting frequency and growth per moult of these early bottom stages.

In two summers' special fishing in Malpeque Bay, P.E.I., MacKay (1919, 1920) succeeded in capturing a total of 573 lobsters, of which 141 ranged from 2⅜ to 4 inches (60 to 102 mm.) in total length. In Malpeque Bay, summer water temperatures are unusually high, often exceeding 21°C. during July and August. Under these conditions hatching would occur earlier than usual and the lobsters, particularly during their first few growing seasons, would moult more frequently. The smallest lobsters (60 to 65 mm.) caught would, according to the Lismore estimate (Table XVI), be in their 11th stage. These lobsters were therefore about one year old, having reached the 9th stage by their first winter and moulted twice during the summer of capture, a moulting frequency only slightly in excess of that estimated for the Northumberland Strait area.

SUMMARY

1. Data are presented on the natural growth of larvae, and on the growth of marked 15- to 25-cm. lobsters, recaptured four to twelve months after release. An attempt has been made to estimate the ages of the smaller commercial-sized lobsters in the Northumberland Strait area.

2. Towing with a plankton net especially designed for the capture of lobster larvae has been conducted in the western part of Northumberland Strait between Richibucto, N.B., and Miminegash, P.E.I., from mid-June to late September each year from 1948 to 1952.

3. During this period a total of 1,599 half-hour surface tows were made during daylight hours at a series of 23 stations. Of the 72,735 larvae captured, 52,403 were in the 1st stage, 11,059 in the 2nd, 5,179 in the 3rd, and 4,094 in the 4th stage.

4. First-stage larvae were abundant from mid-June to the end of August. Fourth-stage larvae were relatively abundant from mid-July to the end of August. Catches during September were relatively small but a few larvae in each stage were taken during the latter half of this month.

5. The growth in length per moult, determined from carapace measurements of representative samples of these larvae, was 34.4 per cent from stage 1 to stage 2, 31.8 per cent from stages 2 to 3, and 30.3 per cent from stages 3 to 4. These estimates agree closely with those presented by Templeman (1948b), but are considerably higher than those given by Hadley (1906) and Herrick (1896). It is concluded that lobster larvae grow more per moult in nature than they do under artificial conditions.

6. Preliminary experiments conducted at Ellerslie, P.E.I., in 1946 and at St. Andrews, N.B., in 1947 showed that a high proportion of lobsters marked by means of holes punched through various sections of the tail fan could be readily recognized after moulting.

7. From 1947 to 1950, eight marking experiments were conducted during April, May and June at six ports in the Maritime Provinces to determine the growth rate under natural conditions.

8. In these experiments, 27,330 lobsters, ranging from about 6 to about 10 inches (15 to 25 cm.) in total length were sorted into five or six ⅛-inch (3.2-mm.) carapace-length groups. These were distinctively marked by means of one or two 3/16-inch (5-mm.) diameter holes punched through various sections of the tail fan and liberated on the fishing grounds off Tignish, P.E.I., Lismore, N.S., L'Archeveque, N.S., Abbott's Harbour, N.S., Port Maitland, N.S., and Grand Manan, N.B.

9. The 2,419 marked lobsters recovered four to twelve months after release show that, within each experiment, growth in carapace length is relatively constant throughout the size range marked. On the average, male lobsters grew slightly more (0.5 mm.) than the females.

10. In the southern Gulf of St. Lawrence, 15- to 20-cm. lobsters (some mature) grew 8 to 9 mm. (13 to 15 per cent) in carapace length, 22 to 25 mm. (13 to 14 per cent) in total length and 80 to 95 grams (45 to 53 per cent) in weight. In southern Nova Scotia and Grand Manan 20- to 25-cm. immature lobsters grew 10 to 12 mm. (13 to 15 per cent) in carapace length, 27 to 34 mm. (12 to 15 per cent) in total length and 170 to 220 grams (43 to 54 per cent) in weight.

11. When the carapace lengths of larvae and 15- to 25-cm. lobsters before moulting are plotted on a double logarithmic scale against the carapace lengths after moulting, the points fall on a straight line. From the equations of these lines and the carapace length of 4th-stage larvae the average carapace lengths of lobsters in stages 5 to 20 were calculated. Equivalent total lengths were calculated from appropriate carapace length–total length equations.

12. These calculations indicate that in the Northumberland Strait area lobsters attain a length of 19 cm. by the 18th stage. Similar calculations for the Bay of Fundy area, more open to question because of failure to catch appreciable

numbers of larvae, suggest that 18th-stage lobsters average 23 cm. in length. These estimates are considerably higher than Hadley's (1906) and considerably lower than Templeman's (1948b).

13. From the seasonal distribution of 4th-stage larvae, from Templeman's data on the effect of temperature on the frequency of moulting and from local water-temperature records, it is estimated that in the Northumberland Strait area lobsters moult five to seven times during their first growing season and pass their first winter in the 6th to 8th stage. Similarly it is estimated that lobsters in this area moult three times during their second growing season and twice during their third, fourth and possibly fifth seasons, the majority passing their second, third, fourth and fifth winters in the 10th, 12th, 14th and 16th stages, respectively.

14. According to these estimates, lobsters in this area reach the 16th stage at the end of the fifth growing season (4¼ years old) at an average length of 14 cm. (5½ in.). Since the majority of lobsters beyond the 16th stage moult only once a year, the 20th stage is not reached until the end of the ninth growing season, when the lobsters are 241 mm. (9½ in.) long and about 8¼ years old.

15. These age estimates are considerably higher than those derived by Hadley (1906) for the American lobster, but agree closely with Dannevig's (1936) estimate for the European lobster.

16. The above conclusions are supported by observations on the growth of planted, artificially reared larvae (Taylor, 1949), and by observations in nature on the early bottom stages.

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APPENDIX

TABLE IV. Carapace length, sex and number of lobsters marked at Seal Cove, Grand Manan, N.B., June 10 to 24, 1947, and of those recovered November 4, 1947, to June 24, 1948. Measurements in thirty-secondths of an inch.

Mid-points of size groups marked	90		94		98		102		106		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	225	261	248	286	244	248	207	222	182	162	1106	1179
Length when recovered												
101								1				
102		2		1			2	2				
103	2	2		1				2				
104	3	2	1	1			1			2		
							———	———[b]				
105		3		2								
106	1	1	2	3	1					1		
107	1	1	2	3					2			
									———	———[b]		
108		1	1	2	1	2						
109			3	2	1	2						
110				2	6		1	1	1			
111			2	3	1	3	1					
112			3	1	2	7	1	1				
113			1	1	4	3	1	1				
114			2	1	1	2	1					
115					2	3	2	2				
116					5	1	2	1	1			
117				1		1	1	3		1		
118							1	1	1	1		
119							1	2	3	2		
120									2			
121								1	1	2		
122									2	1		
123									5			
124									1	2		
125									1	1		
126										1		
127									1	1		
Number recovered	7	12	17	24	24	24	15	18	21	16	84	94
Corrected av. length[a]	104.9	105.9	110.1	108.9	112.7	112.8	115.2	116.6	121.4	121.9		

[a] Since lobsters falling between two graduations were recorded as the smaller, 0.5 has been added to each average.
[b] Lobsters above these lines did not moult and are not included in averages.

Table V. Carapace length, sex and number of lobsters marked at Seal Cove, Grand Manan, N.B., May 23 to June 22, 1950, and of those recovered November 3, 1950, to May 30, 1951. (See Table IV for units and notes.)

Mid-points of size groups marked	90		94		98		102		106		110		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	130	158	258	258	270	266	247	247	232	240	220	231	1357	1400
Length when recovered														
98		1												
99	1													
100		1				1[b]	1							
101	1	3						1						
102	1	3						1						
103	5	9	1				1	1[b]						
104		6	5	7					1	2				
105	1	5	2	2	1				2	3				
106	5	1	5	7	2	2								
107		2	5	2	1	6				1[b]	1			
108	1		6	6	3	3					2	5		
109			6	6	2	4		1			1			
110		1	4	10	6	8	2	1						
111			3	8	6	6	1	2		1		1[b]		
112			6	4	9	12	5	1	3					
113	1		2	1	5	9	2	6						
114		1	2	2	9	6	6	5	2	1				
115			1	1	9	7	6	13		3	1			
116			2		11	7	7	3	4	2				
117			2	1	3	3	5	8	3	2	2			
118			4	1	2	3	3	4		4	1			
119					3		5	5	6		1			
120			1	1		1	6	3	13	3	1	2		
121							7	1	8	6		1		
122							2		5	8	1			
123							1		9	9	2	2		
124							1		1	8	2	3		
125									5	3	3	9		
126									1		6	5		
127										1	6	8		
128											10	4		
129											2	4		
130											2	3		
131											1			
132											1	1		
133											1			
Number recovered	16	33	57	59	72	78	61	56	63	57	47	48	316	331
Corrected av. length[a]	105.1	104.3	110.5	109.7	113.6	112.8	117.4	116.1	120.7	121.5	126.3	126.7		

TABLE VI. Carapace length, sex and number of lobsters marked at Tignish, P.E.I., June 13 to 30, 1947, and of those recovered May and June, 1948. (See Table IV for units and notes.)

Mid-points of size groups marked	68		72		76		80		84		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	155	171	256	257	334	292	258	246	232	245	1235	1211
Length when recovered												
73			1									
			———	——— *b*								
74		1										
75						1						
					———	——— *b*						
76			1									
77			2									
78				1								
79					1							
80					1	1						
81						2						
82			1	2	1	2						
83				1								
84				2								
85					1							
86					1	2						
87					2	1						
88					1	1						
89					2	1		1				
90						2		1				
91							2	1				
92					1	2		3		1		
93										1		
94								1	1	1		
95												
96												
97					1							
98										1		
99					1					1		
100												
101												
102												
103												
104										1		
Number recovered	0	1	5	6	13	15	2	7	1	6	21	35
Corrected av. length[a]		74.5	78.5	82.7	88.2	86.6	91.5	91.9	94.5	97.2		

TABLE VII. Carapace length, sex and number of lobsters marked at Tignish, P.E.I., June 7 to 30, 1950, and of those recovered May 5 to June 27, 1951. (See Table IV for units and notes.)

Mid-points of size groups marked	68		72		76		80		84		88		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	153	233	540	607	617	417	237	211	147	120	93	127	1787	1715
Length when recovered														
74	1													
75														
76		1												
77	2	4		3										
78		1	5	6			1							
79	1	2	2	7		1	1							
80			14	13	1	2								
81			4	14	2	4								
82	1		10	8	4	2			1					
83			7	9	7	7								
84			5	3	6	3		2						
85			2	7	14	5		1						
86					8	9	.1				1			
87					6	9	2	1						
88					5	3	1							
89								6						
90				1	1		6	2						
91							6	6		1				
92							2	3	1					
93							3	1	4	4				
94							2	2	1	1				
95			1				2		4	1		1		
96								1	2	3				
97									2	4	2	2		
98											1	1		
99										1	2	1		
100											3			
101											2	4		
102											2			
Number recovered	5	8	50	71	54	45	27	25	15	15	13	9	164	173
Corrected av. length[a]	78.3	78.0	82.1	81.7	85.4	85.1	91.5	90.6	95.1	95.6	100.2	99.4		

TABLE VIII. Carapace length, sex and number of lobsters marked at Port Maitland, N.S., April 19 to May 31, 1948, and of those recovered November 4, 1948, to May 13, 1949. (See Table IV for units and notes.)

Mid-points of size groups marked	90		94		98		102		106		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	184	235	308	360	334	458	243	276	238	265	1307	1594
Length when recovered												
96	1	1				1						
97					1	1[b]						
98			1	1				1				
99	2		3	1								
100			1	1								
101	1	3	2					1				
102	2	1	2	1			2	1				
103	1					1	3					
104		1		1	2			1[b]		3		
105			2	1	2				1			
106			2		1	1				2		
107				3	2	2			1	1		
108				2	1					2		
109	1		1	1		3			1	1[b]		
110			1	1	3	3						
111				1	4	2						
112				2	2	1		2		1		
113					4		1	2	1			
114						2			1			
115							3					
116					3	1	1	1		1		
117							4	2				
118							1	1				
119							3		1	1		
120							1	1	1	1		
121							1	1				
122												
123												
124												
125										1		
126												
127												
128									1			
129										1		
Number recovered	8	6	15	16	25	18	20	14	8	15	76	69
Corrected av. length[a]	101.9	101.3	103.3	106.7	110.7	110.4	117.7	116.4	119.3	120.7		

TABLE IX. Carapace length, sex and number of lobsters marked at Abbott's Harbour, N.S., April 26 to May 28, 1948, and of those recovered December 1, 1948, to April 26, 1949. (See Table IV for units and notes.)

Mid-points of size groups marked	90		94		98		102		106		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	466	510	578	521	335	319	255	248	275	239	1909	1837
Length when recovered												
100	1	1										
101		4		1								
102		1	1	2								
103	3	3		2								
104	1	3	5	7			1					
								[b]				
105	1	4	1	3								
106	2	3	3	4	1							
107		1	2	3								
108	2		5	3	1							
109			1	5	1	1	1	1				
110			3	7	2	2		1				
111			1	1	6	2	1					
112				2	6	6	2	2				
113			1	1	5	8	3					
114			3		12	6		2				
115					3	4	3	3	1	1		
116			1		3	1	2	2	1			
117						1	6					
118								1	2			
119							5	2		3		
120							1		1			
121							1		2	2		
122								1	3			
123									1			
124										2		
125												
126									1			
Number recovered	10	20	27	41	40	31	26	15	12	8	115	115
Corrected av. length[a]	105.1	104.1	108.6	107.5	113.2	113.5	116.4	115.6	120.8	120.7		

TABLE X. Carapace length, sex and number of lobsters marked at L'Archeveque, N.S., June 2 to July 10, 1948, and of those recovered May 21 to July 15, 1949. (See Table IV for units and notes.)

Mid-points of size groups marked	90		94		98		102		106		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	220	290	363	457	584	740	206	216	177	178	1550	1881
Length when recovered												
90	1	[b]										
91												
92												
93												
94			1									
95			1	2 [b]								
96												
97												
98					2							
99		1	1		3	[b]						
100		1	1									
101	2	1	1									
102	1			1								
103			1	2			1					
104			7	6			3	[b]				
105			3	1								
106			6	3					1	[b]		
107			4	4	1	3						
108				1	4	2						
109			2	1	9	6						
110					2	3		1				
111					7	6	2	1				
112					1	6		2				
113					5	1		1				
114					8	1	2	3				
115					1		1	1				
116							6	3		2		
117							2	2				
118												
119							5	1	1	2		
120												
121									1			
122									2	2		
123									3	2		
124									1			
125									2			
126									4	1		
127									4			
128									1			
Number recovered	4	3	28	21	43	28	22	15	20	9	117	76
Corrected av. length[a]	101.8	100.5	105.4	105.8	111.6	110.7	116.6	114.9	125.1	121.2		

Table XI. Carapace length, sex and number of lobsters marked at Lismore, N.S., June 7 to 30, 1950, and of those recovered May 5 to July 2, 1951. (See Table IV for units and notes.)

Mid-points of size groups marked	68		72		76		80		84		88		Totals	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number marked	247	265	580	732	827	841	542	467	431	457	396	477	3023	3239
Length when recovered														
74		2												
75	1	1												
76	1	4		1		1[b]								
77	1		1											
78	1	4	2	3		1								
79	9	15	3	12		1	1	[b]						
80	7	9	2	6		1								
81	2	4	4	8	1	4								
82	1	1	2	13	2	6		1						
83		2	3	21	6	13		1	1					
84		2	9	10	6	29				1[b]				
85			3	5	3	14		1						
86			1	4	18	20	3	1	1					
87				2	10	14	2	6	1	1				
88				1	7	2	2	5	1					
89		1	1	1	1	7	5	9		1				
90				3	5	2	5	14	1	3				
91					1		4	7	1	2				
92					2		7	8	3	3				
93				2		2	4	7	5	11				
94			2	4			2	3	5	8		3		
95				1				3	2	4		2		
96				2		2		2	4	6		2		
97				1			1	1	1	4	1	2		
98								2	5	1		2		
99							1	1		1	6	6		
100					1		1		2	1	1	8		
101											5	10		
102								1			3	5		
103											3			
Number recovered	23	45	33	100	63	119	38	73	33	47	19	40	209	424
Corrected av. length[a]	79.7	79.9	83.6	84.2	87.0	85.7	91.5	91.4	94.7	94.4	101.1	99.7		

Growth, Maturity, Fecundity and Mortality in the Relatively Unexploited Whitefish, Coregonus clupeaformis, of Great Slave Lake

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(Received for publication October 27, 1952)

ABSTRACT

Ages were determined of 6,571 whitefish for which sizes were recorded. A length–weight relationship, the percentage of both sexes mature at each age, the sex ratio, the proportion of mature females that spawn annually and the relationship between size of fish and number of eggs were determined from smaller samples.

Growth rate is difficult to assess because of net selection, but it seems to be slower than in more southerly lakes. Growth appears to be limited to the period June to September inclusive.

The total annual mortality rate of 61 per cent represents the unexploited condition—four years of commercial fishing with 5½-inch mesh gill-nets produced no obvious change. A moderate mortality rate acting at all ages will easily account for thousands of eggs being produced for every whitefish that survives to maturity—it is unnecessary to assume a low percentage of eggs fertilized or excessive mortality among fertilized eggs or among young fish.

A more intensive fishery would probably increase sustained yield.

INTRODUCTION

Great Slave Lake is of particular interest because, except for an insignificant fishery for local use, the lake was unexploited until recently. It is the only one of the large lakes of North America for which this is true. It is the fifth-largest lake in North America, being smaller than Superior, Huron, Michigan and Great Bear. On the basis of the most recent published aerial survey maps its area is calculated to be 11,070 square miles, of which 10,430 square miles are water and the remainder islands. Its general nature has been described by Rawson (1950).

In 1944 Dr. D. S. Rawson began a four-year program of limnological and fisheries investigations under the auspices of the Fisheries Research Board of Canada. As a result of his recommendations, commercial fishing began late in the 1945 summer season. On the basis of a further recommendation, the Fisheries Research Board of Canada instructed the author to make a detailed study of the effect of the commercial fishery on the fish. This study was initiated at the beginning of the 1946 fishing season and has continued until the present.

The most important commercial fish in the lake is the lake whitefish, *Coregonus clupeaformis*, with which this paper is concerned. Rawson (1951) states that there are at least 21 other species of fish in the lake. Of these other species, the lake trout (*Cristivomer namaycush*) is almost as important a commercial fish as whitefish. Inconnu (*Stenodus leucichthys mackenziei*), pike (*Esox lucius*) and

J. Fish. Res. Bd. Can., 10(7), 1953.
Printed in Canada.

yellow walleye (*Stizostedion vitreum vitreum*) combined constitute about 5 per cent of the commercial catch.

ACKNOWLEDGMENTS

Grateful acknowledgment is made of the indispensable assistance of Messrs. F. M. Atton, R. E. Himsl, T. K. Goodhand, L. C. Hewson, J. A. Dick, L. J. Stephen and D. C. Gibson in collecting the scale samples, and of the careful work of Mr. C. W. Douglas and of Misses L. Bograd and E. J. Johanson in making age determinations.

MATERIALS AND METHODS

A major part of the scales used for age determinations was taken from fish caught by commercial fishermen which are referred to as commercial whitefish. To facilitate analysis of the data, seven scale-collection stations were decided upon. Each station was defined as the water within a radius of five miles of some point on the map of Great Slave Lake. The location and designation of each of the stations is indicated in Figure 1. The stations are numbered roughly from southwest to northeast, that is, from the moderately oligotrophic to the extremely oligotrophic parts of the lake.

Samples of various sizes were taken each year from all the fish caught by the commercial fishermen at any given station. For all practical purposes, the catches that were sampled can be regarded as chosen at random from all the catches, although strictly speaking this was not true, because sometimes convenience determined which catch was used. From each catch sampled, a subsample of about 100 fish—although occasionally subsamples were considerably larger or smaller—was taken at random. One or more subsamples constituted the sample for a given period of time at a given scale-sampling station.

All the commercial whitefish were caught in 5½-inch mesh (stretched measure), in most of which the twine was of 30/6 cotton thread, although in a few it was of finer cotton thread. Seventeen per cent of the subsamples—taken in the earliest sampling—were not taken exactly at any scale-collection station, although they are regarded as part of the sample from the nearest station. They were taken within 30 miles (average distance 14 miles) of the station to which they were assigned.

Each fish in the sample had several scales removed from the region midway between the dorsal fin and the lateral line. The scales were placed in a coin envelope, on which were recorded the date and place of capture and the weight in ounces or in tenths of pounds. Data on sex were not recorded, because the fish were "borrowed" from the owners who did not want the abdomen opened.

Scales were also taken from some of the fish caught in the standard gangs fished by Dr. Rawson's field parties and by the author (these are called standard-gang whitefish). A standard gang consists of 50 yards each of 1½-inch, 2-inch, 3-inch, 4-inch, 5-inch and 5½-inch mesh (stretched measure) gill-nets, and has been described (Rawson, 1951). On the whole, standard-gang whitefish cannot be considered as a random sample of the catch in standard gangs, since in some

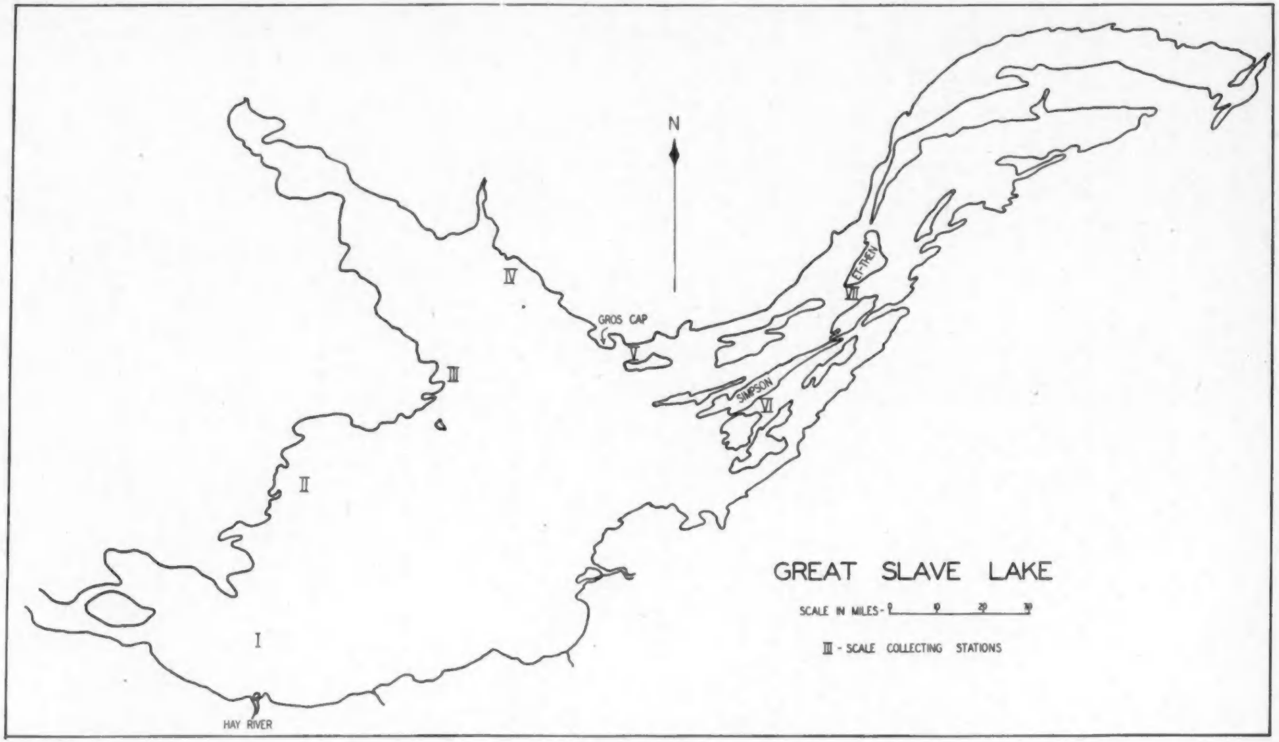

FIGURE 1. A map of Great Slave Lake, showing scale-sampling stations indicated by the Roman numerals.

cases those sizes of fish which are taken less often were deliberately included in the sample in relatively greater numbers than they appeared in the catch. The fish caught by Dr. Rawson's field parties were taken at various places scattered over the whole lake in 1944, 1945 and 1946, while those caught by the author were all taken in the immediate vicinity of Gros Cap in 1946.

Scales were collected from the chosen standard-gang fish in exactly the same way as from the commercial fish, except that in most cases the length (from the tip of the snout to the distal end of the shortest caudal ray), the sex and the state of maturity were also noted on the envelopes.

The scales from both commercial and standard-gang whitefish were examined later in the laboratory to determine age. The procedure was as follows: a few scales were removed from the envelope, cleaned if necessary, and mounted dry between two glass slides. The mounted scales were magnified about 30 diameters (a magnification of 60 diameters was available if required) by means of a projector, and the number of annuli in the projected image were counted. The annuli in Great Slave Lake whitefish are reasonably well defined, and apparently "false annuli" are never formed (presumably as a result of the northern location of the lake). Age determinations were made by technicians who were engaged full-time in scale reading. At least two scales from each fish were used in making a decision regarding age. No scales were disregarded because they were hard to read—a decision was required in every case. Subsequent re-examination of several hundred representative scales has satisfied the author that the final readings assigned by the technicians are correct.

Ages were assigned to 5,321 commercial whitefish and to 1,250 standard-gang whitefish. All these fish were caught in the years 1944 to 1949 inclusive—the time under consideration in this paper.

GENERAL INFORMATION

The subjects included in this section are complementary to the much more intensive studies on growth and mortality. The data used are regarded as adequate for the general treatment of these subjects, but in most cases as too scanty to be worth presenting in detail. Details are on file at the Central Fisheries Research Station, 165 Garry Street, Winnipeg, Manitoba.

The Length–Weight Relationship

For most of the commercial fish, the weight is known but the length is not. It therefore seems desirable to indicate the relationship between length and weight for the benefit of those readers who may be interested in interpreting the results in terms of length.

As mentioned in the previous section, both length and weight were recorded for most of the fish caught in standard gangs. These data have been used to calculate average length and average weight at each age, and points representing the respective logarithms of these averages have been plotted graphically. It was quite obvious that the points all fell on or very close to the straight line whose equation is:

$$\log y = 3.333 \log x - 3.690$$

where: y is the weight in pounds and
x is the length in inches. The relationship can also be expressed as:

$$y = 0.000204x^{3.333}$$

There is no apparent difference between males and females in their length–weight relationship, nor is there a difference between mature and immature fish in this respect.

MATURITY

The whitefish caught during 1946 in standard gangs at Gros Cap were generally examined by the author or occasionally by scientific personnel under his direct supervision. For most of them (those excluded can be considered as randomly chosen), a record was made of whether they were regarded as mature or immature. The basis for calling a fish mature was the examiner's opinion, as a result of a gross examination of the gonad, that the fish had spawned at least once, or that it was going to spawn during the current year. All fish regarded as not falling in either category were recorded as immature.

The proportion of immature to mature fish at each age was determined. The proportion was plotted graphically against age and a free-hand sigmoid curve was drawn which seemed to fit the points reasonably well. From the curve (not shown) the average age at which certain proportions of the fish would be mature were read off and recorded in Table I. The relationships shown in Table I between proportion mature and size were found from similar sigmoid curves

TABLE I. The relation between the proportion of whitefish that are mature, and average age and size, based on the data from a representative sample of 609 caught near Gros Cap, Great Slave Lake, in 1946.

Proportion mature	Average age[a]	Average length	Average weight
%	*years*	*inches*	*lb.*
0	4.0 or less	6.7 or less	0.30 or less
20	8.1	12.1	0.87
40	8.8	13.5	1.21
60	9.6	14.2	1.47
80	10.6	15.0	1.81
100	13.0 or more	18.0 or more	2.78 or more

[a] Note that a fraction of a year has meaning only when average age is considered. Any given fish is, by definition, either mature or immature throughout the entire year that it is a particular age.

which involved length and weight respectively. No difference could be found between males and females with respect to the percentage mature at any size or age.

In addition to the 609 fish (165 mature and 444 immature) used in the above analysis, two fish were disregarded. One was recorded as immature, of undetermined sex, with nineteen annuli, 21½ inches long, weighing 6 pounds, and was omitted because of the probability that the gonad was atropied because of age. The other was recorded as a mature female with two annuli, 6½ inches long and

weighing two ounces, and it was excluded because of the probability that it was a "dwarf whitefish" such as described by Kennedy (1943), because none of the 57 whitefish with three annuli and only one out of the 107 with four annuli were recorded as mature. In view of the comparatively slow rate of increase in proportion of mature among the younger fish, which Table I indicates, it seems possible that at least some of the fish with four and five annuli and perhaps even some older fish in the sample are actually "dwarf whitefish".

Strictly speaking the sample represents only the whitefish in the immediate vicinity of Gros Cap. However, since Gros Cap is in a central location, it seems reasonable to regard the sample as representative of the whole lake. Some observations made by members of Dr. Rawson's field parties, on fish caught by standard gangs at various places on the lake are in agreement with Table I.

Sex Ratio

In the sample of 609 fish just mentioned, the sex was recorded for all of the mature fish and for all but those 159 immature fish whose gonads were too undeveloped to indicate sex on gross examination. Of the immature fish in which sex could be determined, 137 were males, 148 females, and of the mature fish (excluding 6 possible "dwarfs"), 81 were males, 78 females.

In 1946 the author also determined and recorded the sex of the mature whitefish in six random samples of commercial whitefish, where the samples originated in several places scattered over an area of 2,000 square miles in the central part of the lake. These samples did not differ significantly among themselves in sex ratio ($P = 0.5$) and in them there was a total of 233 males and 241 females.

Combining all three sets of values given above produces a random sample of 451 males and 467 females. These values are not inconsistent with the hypothesis that the ratio of males to females is 1:1 ($P = 0.1$).

Frequency of Spawning

Regarding the lake trout of Great Bear Lake, Miller and Kennedy (1948) report ". . . we noticed that many large fish appeared to be immature, whereas other fish, sometimes smaller, had gonads which were almost ripe. It was not until quite late in the season that we realized these large, apparently immature fish were probably mature trout which would not spawn that season. In other words the trout ordinarily do not spawn every season". Dr. D. S. Rawson (personal communication) feels that the same phenomenon probably prevails among the lake trout of Great Slave Lake. Fry (1949) mentions what is essentially the same condition in lake trout from Lake Opeongo, Ontario. Sprules (unpublished manuscript report) noted regarding the Arctic char, *Salvelinus alpinus* at Term Point, Hudson Bay: "It is probable that the char do not spawn every year after maturity is reached and thus certain specimens represented as immature in this report actually may be mature". Kennedy (1949) reported that there was evidence of a similar tendency in the ciscoes *Leucichthys artedi* and the whitefish from Great Bear Lake. Thus a tendency to spawn at intervals of two or more

years may well be the usual thing in many northern freshwater fish populations—possibly because of the short growing season.

Apparently Great Slave Lake whitefish can also be regarded as not spawning every year after they reach maturity. The author found on examination that there were two easily distinguished conditions of the gonad among mature fish. In some cases the gonad appeared practically the same as it does at spawning time (just before actual spawning). Such fish were recorded as "large eggs" and it was assumed that they were going to spawn during the current year. In other cases the largest eggs were noticeably smaller; the whole gonad was intermediate in size between that of an immature female and a female with "large eggs", but often small enough to be mistaken by the unwary for an immature gonad; the tissue was ruptured as in ovaries of spent fish which are in this respect unlike the ovaries of fish that have never spawned; and there were frequently a few large degenerating eggs apparently retained from a previous spawning. These fish were recorded as "small eggs", and it was assumed that they were fish that had spawned some time but which were not going to spawn during the current year.

Of the whitefish for which the data were recorded, 38 were classified as "large eggs", 38 as "small eggs"—that the ratio is exactly 50:50 is a coincidence. So it seems apparent that, on the average, in any one year only one-half of the whitefish represented by the sample spawn, or in other words, that individual fish spawn more or less every other year. Casual observations made by other investigators at other points on the lake are not inconsistent with the hypothesis that Great Slave Lake female whitefish spawn every other year.

The nature of the testes is such that a similar study for male fish is not possible, but the fact that some testes were larger than others in fish of the same size suggests the possibility that at least some males do not spawn every year.

Egg Counts

Eighteen commercial whitefish from the vicinity of scale-collection Station III and three from the vicinity of Station VII were used for egg counts. All were caught on August 14, 1950, and all were mature females with "large eggs". The fish were selected to give a wide range of size, but apart from this they were taken at random.

Each fish was weighed, a scale sample was taken, and then the abdomen was opened and the ovaries were removed, labelled and hardened in formalin. The "egg counts" were made a few days later as follows: The volume of each pair of ovaries was determined by noting the amount of liquid that they displaced when immersed in water in a graduate. Then a small piece of tissue containing about 200 eggs was cut out of the middle of one ovary and its volume was likewise determined. In this small piece all the large eggs (i.e. those which it was assumed would be spawned during the current year) were then separated from the rest of the tissue and counted. The number of eggs in the whole gonad was calculated on the assumption that the ratio between the two volumes is the

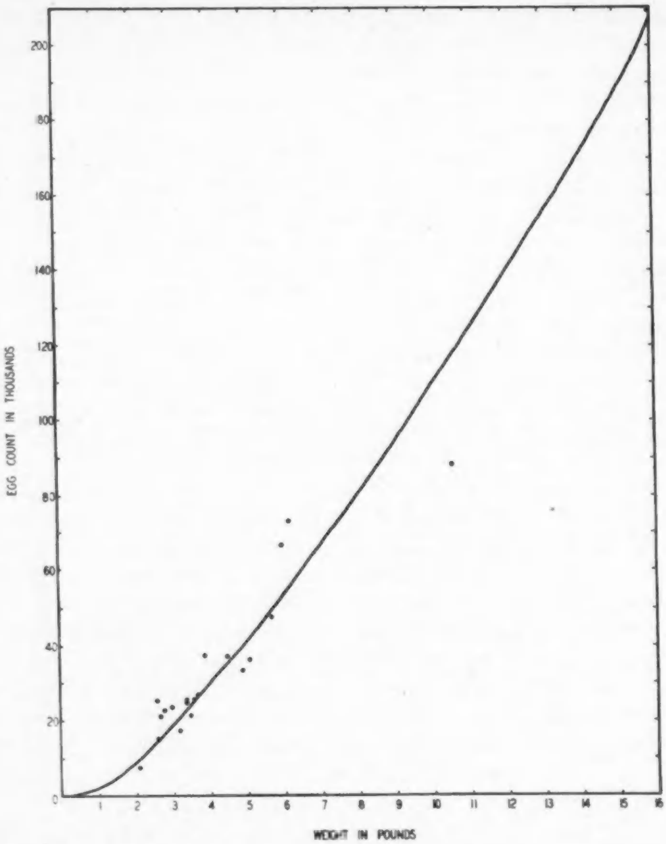

FIGURE 2. The relationship between the average weight of Great Slave Lake mature female whitefish which will presumably spawn during the current year and the estimated number of eggs per fish.

same as the ratio between the respective egg counts. Figure 2 shows the relationship between average weight of mature spawning females and the estimated number of eggs per fish.

SEASONAL GROWTH

Figure 3 shows diagrammatically the relative positions of the outer annuli on the scales of typical Great Slave Lake commercial whitefish taken at four different times during the year. If a straight edge is placed on the projected images of such scales so that it lies along the dorsoventral diameter and through the focus of the scale, and if the following distances are measured along the straight edge: AB between the outside of the scale and the outer annulus, BC between the

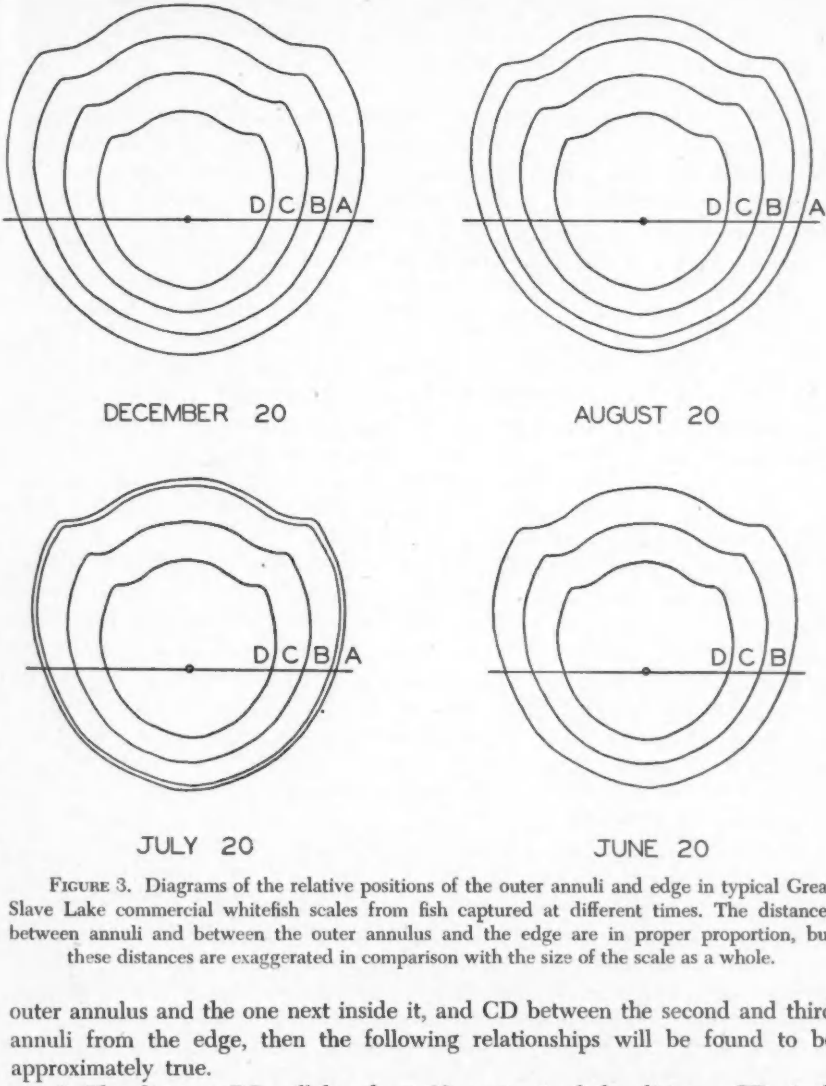

FIGURE 3. Diagrams of the relative positions of the outer annuli and edge in typical Great Slave Lake commercial whitefish scales from fish captured at different times. The distances between annuli and between the outer annulus and the edge are in proper proportion, but these distances are exaggerated in comparison with the size of the scale as a whole.

outer annulus and the one next inside it, and CD between the second and third annuli from the edge, then the following relationships will be found to be approximately true.

1. The distance BC will be about 90 per cent of the distance CD at all seasons.

2. The distance AB will be about 90 per cent of BC on December 20, about 70 per cent on August 20, and about 20 per cent on July 20.

3. The June 20 scales will be indistinguishable in appearance from those of December 20.

In a series of scales taken throughout a given summer, the distance *AB* is greater in scales collected on a given date than on scales collected on some earlier date. By examining scales taken at successively earlier dates it becomes obvious that in typical scales taken on June 20, AB equals zero. In other words, up until that date the dorsoventral diameter of the scale has not yet started its growth for the current year. Rough comparisons of the distances *AB* at various times demonstrate also that, shortly after June 20, typical scales do start to grow in this respect, that they grow rapidly during July and August, and that by approximately the end of September growth ceases.

Some Great Slave Lake whitefish spawn as early as September and others as late as January. Therefore, the "birthday" of any given commercial whitefish could be any time over a period of several months. In this paper for the sake of convenience they are all assumed to have their "birthday" on May 1. In reading the scales, fish captured in June whose scales show x annuli are regarded as $x+1$ years old while those captured in December (also January, February and March) whose scales show x annuli are regarded as x years old. A fish captured in July which shows x annuli is regarded as x years old and called "age x", if distance AB is small compared to BC. It is regarded as $x+1$ years old and called "age $x+1$" if distance AB is approximately the same size as BC (in which case presumably growth has not yet started for the current year).

There is always the possibility that a fish captured early in the summer will be one whose scales have grown unusually fast during the current year, in which case AB may be nearly enough the same size as BC that the scale reader mistakes AB for the total growth made during the preceding year, and classifies it as a year too old on the assumption that annual growth has not yet started in that particular fish. Similarly a fish whose scale growth has not yet started (i.e. AB is zero), in which case CB is unusually small, could be mistaken for one in which there had been some growth during the current year. Such a fish would be recorded as one year too young. It is the author's opinion that errors from these causes are negligibly few.

The rate at which scale size increases during the summer was studied systematically. For this purpose, for each time and place (no two samples at one place were used that were taken less than about one week apart) where sufficient material was available, a sample of the scales from 20 commercial whitefish which were either 12, 13 or 14 years old was taken at random. On the projected images of these scales, magnified 60 times, the distances AB, BC and CD (see Figure 3) were measured. The ratios AB/BC and BC/CD were then calculated for each fish, and the average values of these ratios were found for each sample of 20 fish. These averages, expressed as percentages, are shown in Table II.

For each sample of 20 fish, the average ratio AB/BC is shown in column 3. This ratio compares the average growth made up to the date of capture with the amount made during the whole previous year, and it is, therefore, a measure of the relative amount of growth made during the current year. A better measure of relative amount of growth during the current year would be one which takes account of the fact that during each year there is less growth than during the

TABLE II. Calculated scale growth based on samples each of which consists of scales from 20 representative 12-, 13- or 14-year-old whitefish taken at the indicated time and place from Great Slave Lake.

Station	Date	Average ratio AB/BC[a] %	Average ratio BC/CD[a] %	Calculated % of year's growth to date	% of fish showing growth current year
I	June 29/49	0	90	0	0
I	July 12/49	3	..	3	10
I	Dec. 22/49	79	94	86	100
I	Jan. 4/49	96	85	104	100
II	July 18/49	12	83	13	30
II	July 24/49	16	90	18	45
II	July 30/49	38	96	41	95
II	Jan. 29/50	89	..	97	100
III	July 8/49	0	105	0	0
III	July 20/49	14	101	16	45
III	July 15/48	10	92	11	45
III	July 30/47	25	92	28	75
III	July 18/46	22	88	24	90
IV	Aug. 29/49	69	108	75	100
IV	July 7/48	9	85	9	40
IV	July 13/48	14	81	16	55
IV	July 13/47	9	85	10	45
IV	Aug. 13/47	51	98	56	100
IV	Aug. 25/47	75	88	82	100
IV	July 2/46	19	92	21	65
IV	July 10/46	12	82	14	50
V	June 28/48	7	88	8	45
V	July 7/47	3	86	3	15
V	Aug. 14/47	64	90	70	100
V	Aug. 24/47	75	92	82	100
VI	July 25/49	46	94	50	100
VII	Aug. 10/49	52	100	56	100
VII	Aug. 19/49	55	89	60	100
VII	Aug. 30/49	53	101	58	100
VII	Aug. 22/47	56	93	62	100

[a] See Fig. 3 for explanation of AB, BC and CD.

previous year (i.e. the ratio AB/BC cannot become 100 per cent in a typical case). Therefore, values for the ratio BC/CD given in column 4 were calculated. The grand average of these ratios is 91.7 per cent. The values given in the fifth column of Table II are the values of the third column divided by 91.7. They represent the average proportion of the current year's growth made prior to capture as a percentage of the total growth expected during the year on the basis of the amount of growth in the two previous years. The last column of Table II shows the proportion of fish in the sample in which the appearance of the scale is interpreted as showing some growth during the current year. Although some fish show evidence of growing in late June, others apparently do not start growing until early August.

The values for the ratios BC/CD tend to have a normal distribution about their mean value of 91.7 per cent. There is no demonstrable tendency for the values for any given year or for any given place to be predominantly greater or

less than the over-all average value. The lack of any tendency for values of the ratio BC/CD to be influenced by time or place is the reason for choosing to divide the values of the ratios AB/BC by the grand average of the values of the ratio BC/CD, rather than by the corresponding individual values of BC/CD, to get the values in the fifth column of Table II.

Values from the fifth column of Table II are plotted against the corresponding dates, disregarding the year of capture, in Figure 4. The curve shown in Figure 4 is that free-hand curve, which, of several such curves tried, makes the sum of the squares of the distances from the various points to that curve a minimum. The points for December and January were disregarded on the assumption that by December all fish would have completed their current year's growth. The curve shows that the scales of Great Slave Lake commercial whitefish increase in diameter only from the middle of June until the end of September, and that almost one-half of their growth for the year takes place in the first two weeks of August. It is interesting to note that there is growth only during the time that water temperatures are relatively high, and that the fastest growth occurs when water temperatures are at or near the annual maximum (see Rawson, 1950).

All the points in Figure 4 which collectively represent any one year or any one place tend to be randomly distributed about the line. There may be a tendency for growth to start later in those parts of the lake where water temperatures are colder, and fish caught in 1949-50 may have been predominantly slower than usual to start growth, but in neither case can the departure from a distribution of half above, half below the line be shown to be statistically significant. In other words, no variation in growth pattern which depends on calendar year or place of capture can be demonstrated with the available data. The curve of Figure 4, therefore, can be regarded as representing the average growth of commercial whitefish scales at each of the seven stations and for each of the four years considered.

The possibility that the annual growth pattern differs with age was explored. For this purpose, all the scales taken from standard-gang whitefish caught were considered, and from them scales from all suitable fish in the three categories, 4- and 5-years-old, 7- and 8-years-old, 12-, 13- and 14-years-old, were treated as described above for the scales from the commercial fish. Mainly because most of the good samples were collected in June, the amount of useful data was disappointingly small and too meagre to be worth presenting. Such as they are, the data indicate that probably the 4- and 5-year-old fish start growing first, the 7- and 8-year-old fish next and the 12-, 13-, and 14-year-old fish last.

It is a commonly accepted theory that there is a simple positive relationship between the growth of many fish, including whitefish, and the growth of their scales. On this basis, Figure 4 could be regarded as representing, not only the annual growth pattern of the dorsoventral scale diameter, but also the pattern of growth in, say, weight of typical Great Slave Lake whitefish. It is, in fact assumed here that the percentage of the current year's growth in weight which the average fish has added by any given date equals the percentage of scale growth indicated by the curve in Figure 4.

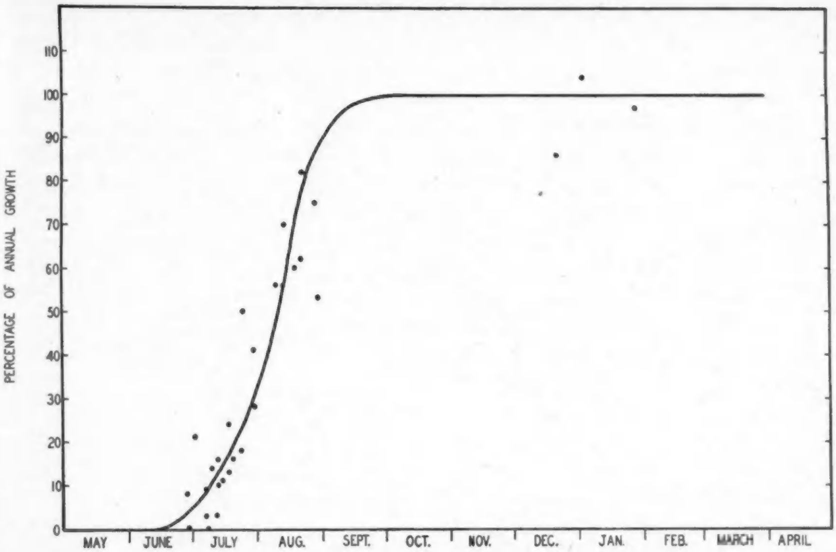

FIGURE 4. The average amount of growth in dorsoventral scale diameter made during the year by samples of Great Slave Lake whitefish captured at various times, where the amount of growth is expressed as a percentage of the growth expected during the year had the fish not been captured.

MORTALITY RATE

The mortality rates that prevail in a population of fish can be estimated if the ages of a random sample are known. The technique has been reviewed by Ricker (1948). The underlying principle is: when those fish are disregarded which are too small to be taken with full efficiency by the particular gear used, then generally the number of fish in each age-class is less than the number in the next youngest year-class (this is not true where there are violent fluctuations in year-class strength). The obvious explanation is that the number of fish in any age-group diminishes from year to year as a result of deaths from various causes. The observed rate of decrease within the sample is regarded as representing the annual mortality rate in the population, that is, the proportion of fish which die each year. In practice, mortality rates are determined graphically from "catch curves". Catch curves are derived by plotting the logarithm of the number of fish of a given age against their age.

All data available for calculating mortality rates among Great Slave Lake commercial whitefish are given in Table III, which shows the number of fish of each age in random samples from commercial catches made at various scale-sampling stations during the period 1946-1949. Figure 5 shows catch curves based on the data from scale-sampling Station IV for each of the four years. These catch curves are typical in that they have an ascending left limb and a

TABLE III. The number of fish of each age in representative samples of Great Slave Lake commercial whitefish.

Station	Year[a]	Age 8	9	10	11	12	13	14	15	16	17	18	19	20	over 20
I	1948	0	19	26	53	28	24	3	4	1	1	0	1	0	0
I	1949	1	1	21	65	124	135	152	114	65	34	14	6	1	1
II	1949	1	10	31	77	101	103	71	45	22	8	1	0	1	0
III	1946	0	0	3	17	28	25	20	1	1	1	0	0	0	0
III	1947	0	0	1	6	11	8	6	2	3	1	2	0	0	0
III	1948	0	0	8	17	23	22	25	13	7	3	0	1	0	0
III	1949	0	0	2	11	41	80	105	120	73	43	20	8	2	2
IV	1946	0	0	35	77	133	72	32	2	3	0	0	0	0	0
IV	1947	0	21	53	125	109	69	24	7	2	5	0	2	0	1
IV	1948	0	1	14	55	112	66	41	8	4	1	0	0	0	0
IV	1949	1	5	32	67	140	141	81	30	11	6	2	0	0	0
V	1947	1	5	21	82	128	79	46	23	11	10	3	0	0	0
V	1948	0	0	2	1	6	21	19	6	8	2	2	1	0	0
VI	1949	0	0	4	6	30	80	107	104	101	65	20	8	5	2
VII	1947	0	1	2	18	29	23	10	8	2	0	0	0	0	0
VII	1949	1	2	8	19	43	77	94	69	79	59	29	14	7	1

[a] The year actually extends from May 1 of the calendar year shown to April 30 of the following calendar year.

dome which represent age-classes that are not fully vulnerable to the fishing gear, and a descending right limb which, starting at about age 14, is more or less a straight line, and which represents the decrease in number from year-class to year-class, in other words, the annual mortality. In Figure 5 there are two isolated points to the right of the 1947 curve. These have not been connected with the rest of the curves because of a peculiarity of logarithms. The nature of logarithms is such that values for zero fish would be plotted at an infinite distance below the graph. The catch curve, if continued, would drop perpendicularly from the right end of the curve for an infinite distance to the value for zero fish at age 18, then rise perpendicularly to the point shown for age 19, then drop perpendicularly for an infinite distance to the value for zero fish at age 20, then rise

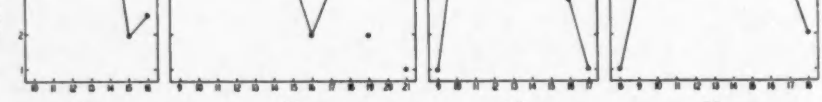

FIGURE 5. Catch curves for the samples of commercial whitefish taken at scale sampling Station IV, Great Slave Lake during the first four years of exploitation.

perpendicularly to the point shown for age 21, and finally drop perpendicularly to the value for zero fish at age 22.

Inspection of Figure 5 and Table III shows that year-classes of Great Slave Lake whitefish tend to be of equal strength.

Figure 5 indicates that there has been no recent increase in mortality rate. Ricker illustrates the effect that such an increase has on an individual catch curve based on samples taken several years after the actual increase. None of the curves in Figure 5 show the characteristics of such a curve. Furthermore, using Ricker's techniques, the calculated mortality rate for 1946 was highest, that for 1948 next, for 1947 next and for 1949 lowest, in other words mortality rate seemed to decrease if anything. Since it is incredible that fishing could bring about a *decrease* in mortality rate, these apparent changes are regarded as the result of either chance variations from sample to sample or of the fact that the average depth at which fishermen fished at Station IV increased slightly over the four years. On the basis of general experience with coregonine fish, fishing deeper would be expected to increase the proportion of older fish, which would give the appearance of a lesser mortality rate.

If commercial fishing had caused total mortality rate in any part of the lake to increase, it should have been among the fish represented by scale-sampling Station IV. More than one-quarter of all the fish taken prior to 1949 were taken from the one-sixteenth of the lake's area that lies nearest to Station IV. Since the disproportionately heavy exploitation of this particular population produced no measurable change in mortality rate, there seems to be no reason for suspecting a change in the lake as a whole between 1945 and 1949. The data shown in Table III for stations other than Station IV also fail to indicate any definite change during that time.

If there has been no change, then all the data for each scale-collection station can be combined regardless of year of capture. If catch curves were drawn using this combined data, the annual mortality rates derived from them would be approximately as follows: for Station I, 0.54 (i.e. among the larger fish, for every 100 fish alive at a given time, 54 are expected to die during the next year); for Station II, 0.59; for Station III, 0.60; for Station IV, 0.63; for Station V, 0.51; for Station VI, 0.59; and for Station VII, 0.52. The apparent differences in mortality rates from place to place may be real, but the fact that there is no obvious pattern which depends on the relative positions of the stations, and the fact that mortality rate may vary considerably among subsamples taken at various times within the same year at any given station, indicate that the differences probably represent normal variation.

On the assumption that the whole population is homogeneous with respect to annual mortality rate, all the data in Table III except that for Station VII were combined to give the catch curve shown in Figure 6A. Even if this assumption is incorrect, Figure 6A is a proper catch curve, since the number of fish in each sample was roughly proportional to the number in the commercial catch from the area represented. Scale-sampling Station VII was excluded because the fish taken there were predominantly of the type described by Rawson (1947) as:

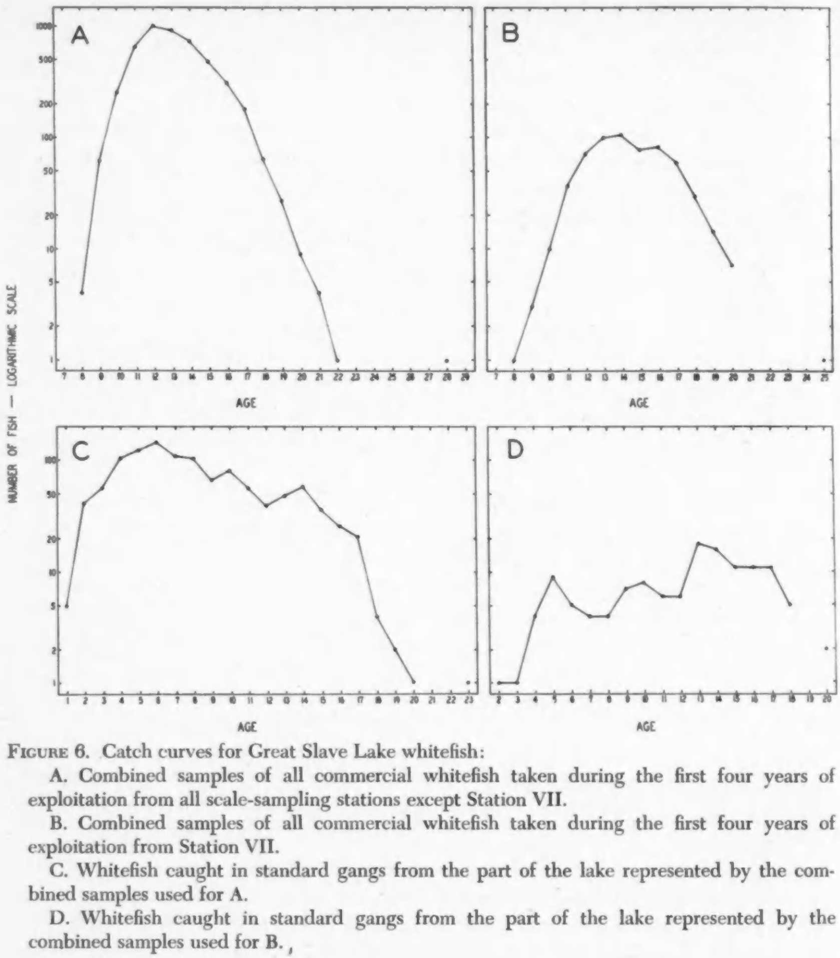

FIGURE 6. Catch curves for Great Slave Lake whitefish:

A. Combined samples of all commercial whitefish taken during the first four years of exploitation from all scale-sampling stations except Station VII.

B. Combined samples of all commercial whitefish taken during the first four years of exploitation from Station VII.

C. Whitefish caught in standard gangs from the part of the lake represented by the combined samples used for A.

D. Whitefish caught in standard gangs from the part of the lake represented by the combined samples used for B.

". . . of somewhat darker colour, longer and more compressed bodies and softer flesh". There is some doubt whether these fish (locally called "black whitefish") should be regarded as identical taxonomically with other *C. clupeaformis.*

If commercial fishing had caused the mortality rate to increase during the period 1945-1949, then even though the curve is a composite of four year's fishing, the right limb of Figure 6A should have been concave. Since it is not, it serves to further confirm the conclusion that, on the basis of the data available to the end of 1949, no effect of the commercial fishery on mortality rate can be demonstrated.

The catch curve of 6A is interpreted as follows: All age-groups less than 17 years old are caught with less than maximum efficiency. The points which repre-

sent the remaining year-classes fall very nearly on a straight line (any deviation from the straight line is presumably the result of chance variation). The slope of this straight line represents the rate at which the number of fish is diminishing. By using Ricker's technique, the annual mortality rate represented by this straight line can be calculated. It was found to be 0.61 over the range in ages 17 to 22 years, inclusive. It is important to note that, since no change in mortality rate could be demonstrated over the whole time that the lake has been exploited, the value *0.61 represents the mortality rate before there was any commercial fishing*, that is, it represents the natural mortality rate. In other words, 61 per cent of the larger fish would die each year if the lake were not fished at all.

Figure 6B represents all of the fish in the various samples taken at Station VII. The dome of this catch curve is considerably more flattened than is that of the curve shown in 6A. The flattening cannot be accounted for by differences in the size of individual fish, since, as will be shown in the next section, the average whitefish at Station VII is the larger. It is assumed that the flatness of the dome is the result of more immigration than emigration of whitefish of the ages under consideration, in the general area represented by Station VII, because there is not enough successful spawning in the area to produce all the whitefish the area can support. This assumption is in accordance with the facts that there are relatively few whitefish in the general area, and that they are generally appreciably larger than average. Although immigration of whitefish presumably plays an important role in determining the age composition in the sparsely populated east end of the lake, the emigration of these same fish from the other parts probably has little effect because of the much higher concentration of fish in the latter. This idea is not inconsistent with the conclusion, drawn as a result of recapturing tagged fish, that the average Great Slave Lake whitefish tends to remain within a few miles of one place, since the migrants are, in a sense, atypical. The fact that the whitefish in the east end are predominantly "black whitefish" can be fitted into this hypothesis in various ways depending on what assumptions are made regarding the exact nature of the phenomenon "black whitefish". Mr. R. R. Wheaton is currently investigating this phenomenon.

When Ricker's technique is applied to the right limb of the catch curve, for Station VII (i.e. Figure 6B) the calculated mortality rate is 0.52. The difference between this value and the value 0.61 for the remainder of the lake can be explained in either (or both) of two ways: (1) it is an effect of continued recruitment because of immigration, or (2) it is an effect of lessened competition because of the much sparser population.

Figure 6C shows the catch curve for all the standard-gang whitefish that were taken in the part of the lake represented by Stations I, II, III, IV, V and VI, and Figure 6D shows the same for Station VII. Both show a greatly extended dome. It might be suspected that this was a result of the fact that, in these particular samples, the proportion of fish of the sizes that were taken in greatest abundance in the sample was, as mentioned above, less than the proportion in the catch. However, examination of the data shows that this factor by no means accounts altogether for the shape of these curves. The real reasons for the par-

ticular shape seem to be that various mesh sizes were used to get the fish, each of which, as Rawson (1951) shows, captured a characteristic size (hence age) range of fish, and that, for some reason, the mesh sizes that take the smaller fish do not catch nearly as many fish for a given number present as do those meshes that take larger fish.

Figure 6C and 6D indicate that the standard-gang fish which are caught with maximum efficiency are of the same range in age as are the corresponding commercial fish. The mortality rates indicated by the catch curves for standard-gang fish are about the same as those indicated by comparable catch curves for commercial fish.

A comparison of 6C and 6D adds some further weight to the hypothesis that fish migrate into the east end of the lake (i.e. into the area represented by 6D).

Before closing this section, some discussion of the applicability of Ricker's technique to catch curves from gill-nets seems in order. A gill-net is a fence of fine netting which catches fish by ensnaring them, presumably because they are unaware of the danger and blunder into the web of the net. In most cases any fish that is caught is ensnared specifically because it passes part way through a mesh and cannot get any farther. It becomes wedged in that mesh (no doubt the fact that the first contact with the mesh must startle the fish and cause it to lunge forward greatly aids this wedging) so that it is unable to free itself by the relatively weak swimming motions that it can make in reverse. Since whitefish taper forward from the middle of the body to the snout, there will be a wide range in sizes of fish for which the girth at some point on the taper will cause the fish to become wedged into a given mesh size. Presumably the left limbs and domes of the various catch curves presented represent cases where the maximum girth of some of the fish in the age-group is too small to prevent them from going completely through the mesh. The question then arises: if there is a minimum size of fish which the mesh will ensnare, is there also a maximum size? Rawson's (1951) Figure 6 is very informative in this respect. It shows that although a given mesh size catches whitefish of a characteristic size range, it also catches a few that are practically as big as the biggest taken (these fish are caught by the mouth parts). When the relative abundance of the various sizes is considered—it can be assessed by producing the right limb of the catch curve backwards—it seems evident that a given net tends to catch the largest fish with greater efficiency than it catches the others. It is also evident from the same data that the importance of this effect diminishes as mesh size increases until it is an insignificant factor in 5½-inch mesh—the mesh size used to catch the commercial fish. Thus, the effect is the opposite of what would be observed if there were a maximum size which the net will take. The increased efficiency in catching fish of the size that are caught by their mouth parts probably results from the fact that a fish approaching the net from any angle can be so captured, whereas one that is ensnared by the more usual method must approach the net approximately at right angles to it. The limited data available for ages of fish in specific mesh sizes agree with the above data of Rawson.

The fact that one age-28 fish in Figure 6A and one age-25 fish in Figure 6B

fall so far off the respective right limbs of the catch curves may be explained by this tendency to catch disproportionate numbers of the largest fish. However, since only one fish is involved in each case, sampling error is also a possibility. The fact that the biggest fish are caught with increased efficiency may obscure a tendency for mortality rate to increase among the oldest fish. Presumably there must be such a tendency since it is impossible for fish to live forever.

GROWTH RATE

Table IV shows the average weight at various ages of all the commercial whitefish sampled. In the case of most of the scale-sampling stations, the values given represent averages based on two or more years. This seems justified, since a preliminary comparison of the averages for individual years at the various stations showed no evidence of progressive changes that could be interpreted as either increases or decreases in rate of growth during th period 1946-1949.

TABLE IV. The relationship between age and average weight in pounds in representative samples of Great Slave Lake commercial whitefish caught during 1946–1949. Only averages based on 20 or more fish are included.

	Sampling stations						
Age	I	II	III	IV	V	VI	VII
9	1.9	..	..	2.1	..	..	..
10	2.1	2.2	..	2.2	2.3	..	..
11	2.4	2.3	2.5	2.4	2.5	..	2.9
12	2.5	2.6	2.6	2.7	2.9	3.0	3.1
13	2.7	2.6	2.8	2.9	3.2	3.1	3.3
14	2.7	2.8	3.0	3.2	3.6	3.3	3.7
15	3.1	3.0	3.1	3.3	4.0	3.5	4.1
16	3.3	3.1	3.5	3.5	..	3.5	4.7
17	3.8	..	3.7	..	..	3.7	5.0
18	..	..	3.6	..	..	3.9	5.4
Fraction[a]	0.62	0.54	0.14	0.46	0.47	0.23	0.75

[a]Actual age was greater than the designated age by some fraction of a year; therefore, the average weight must have been greater than at the birthday. The values listed in this row indicate the average fraction of a total year's growth made by the respective samples.

Since most of the fish had grown since their "birthday", then obviously the average weight at the time of capture was greater than if the fish had been exactly the designated age. The proportion of the current year's growth that any individual fish has made up to the time of capture can be estimated from Figure 4. To make exact comparisons possible, the estimated average proportion of the current year's growth for all the fish in each of the samples is shown in the last line of Table IV. Supposing, for instance, that the samples from Stations I and III are being compared, then it should be kept in mind that the average weight at Station I includes 62 per cent of the weight likely to be added during the current year, whereas that at Station III includes only 14 per cent.

Table IV indicates that there is a slight increase in rate of growth from

Station I to Station VI, with perhaps a more pronounced increase to Station VII. This represents an increase from southwest to northeast, from the moderately oligotrophic condition to the extremely oligotrophic. There is no obvious explanation for such a gradation.

Table V shows the size distributions by ages of all the commercial whitefish

TABLE V. The number of fish of a given age which are of a given weight in all representative samples of whitefish taken by commercial fishermen near scale-collection Stations I, II, III, IV, V, and VI, Great Slave Lake from 1946 to 1949.

Wt. in lbs.	Age in years[a]															
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	28
1	1	..	..	..	..	..	..	..	..	..	..	..	..	..		..
$1\frac{1}{4}$	1	1	2	..	2	..	..	..	..	..	..	..	..	..	..	..
$1\frac{1}{2}$	1	4	10	4	4	2	1	..	..	..	..	..	..	..	..	..
$1\frac{3}{4}$	0	11	18	18	11	5	3	..	1	..	..	..	..	..	..	..
2	0	26	70	85	46	22	15	4	1	..	..	..	..	..	..	..
$2\frac{1}{4}$	1	17	97	186	126	61	57	21	5	1	1	1	..	..	..	..
$2\frac{1}{2}$	..	3	35	211	299	148	60	41	16	1	3	0	..	..	..	..
$2\frac{3}{4}$	..	..	15	115	273	177	117	58	28	7	3	0	1	..	..	..
3	..	..	6	24	165	281	136	86	45	26	3	2	0	..	..	..
$3\frac{1}{4}$	..	..	..	9	63	128	136	89	41	23	7	5	0	..	..	..
$3\frac{1}{2}$	..	..	..	5	17	79	117	61	61	25	8	2	0	..	1	..
$3\frac{3}{4}$	..	..	..	0	3	14	55	39	33	30	10	3	0	..	..	..
4	..	..	..	1	4	4	27	45	35	20	5	3	1	..	..	..
$4\frac{1}{4}$	..	..	..	1	1	2	5	21	19	19	4	1	2	2	..	..
$4\frac{1}{2}$	..	..	..	..	..	1	2	9	18	13	4	1	3	1	..	..
$4\frac{3}{4}$	..	..	..	..	..	1	1	3	6	6	5	2	0	1	..	..
5	..	..	..	..	..	..	..	1	3	5	6	2	1	..	..	..
$5\frac{1}{4}$	..	..	..	..	..	..	..	0	..	2	1	0	0	..	..	..
$5\frac{1}{2}$	..	..	..	..	..	..	..	0	..	0	1	3	0	..	..	..
$5\frac{3}{4}$	..	..	..	..	..	..	..	0	..	0	3	0	0	..	..	..
6	..	..	..	..	..	..	..	0	..	0	..	1	0	..	..	..
$6\frac{1}{4}$	..	..	..	..	..	..	..	1	..	1	..	0	0	..	..	..
$6\frac{1}{2}$	..	..	..	..	..	..	..	..	..	1	..	1	0	..	..	..
$10\frac{1}{2}$	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
$12\frac{3}{4}$	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1

[a] The average fish is older than the exact age given by enough to cause an estimated 42 per cent of the current year's growth.

in all the samples combined, except those which were taken at Station VII. Separate consideration is given to Station VII, because as outlined above in connection with mortality rates, they seem to be a separate population. The table illustrates the considerable range in size among fish of a given age. The largest are as much as five times as heavy as the smallest.

In Table V a comparison of size distributions among the age-groups indicates net selection among the younger fish (all less than age 14 and perhaps others) since the upper size limits increase considerably with age but the lower limits do not. Net selection is still more obvious when the effect of mortality is considered. If the mortality rate 0.61 is assumed to apply to younger ages, then every unit of the population which contains the number of fish that are 17 years and older in Table V must also contain approximately 350,000 fish of age 9 (this value can be determined graphically by extrapolating the best straight line through

the right limb of the curve in Figure 6A). It is therefore apparent that only a minute proportion of the age-9 fish are caught in comparison with the proportion of those that are, say, age 17. Presumably those caught are only the very largest representatives of the year-class, and even they may not be taken with full efficiency. The fish captured are probably at least as atypical of the actual size distribution as is the 10½-pound individual among the age-20 fish.

Table VI shows the size distribution by ages in the samples of commercial whitefish taken at Station VII. A comparison of Table VI and Table V gives further evidence that growth rate is considerably faster near Station VII than elsewhere on the lake. The fact that the smallest fish captured are considerably bigger than the smallest indicated by Table V is further evidence for an hypothesis stated in the previous section, namely that there is inadequate spawning

TABLE VI. The number of fish of a given age which are of a given weight in all representative samples of whitefish taken by commercial fishermen near scale collection Station VII, Great Slave Lake from 1946–1949.

Wt. in lbs.	Age in years[a]													
	8	9	10	11	12	13	14	15	16	17	18	19	20	25
1¾	..	..	..	..	..	..	1	..	..	..	..	..	..	..
2	..	2	1	..	..	..	0	..	..	..	..	..	..	..
2¼	1	1	1	6	2	..	0	..	..	..	..	..	..	..
2½	..	..	1	8	8	5	3	..	..	..	..	..	..	
2¾	..	..	0	7	12	16	6	2	..	..	..	..	..	..
3	..	..	3	6	23	20	13	3	2	..		..	..	..
3¼	..	..	4	3	12	23	14	6	4	..	..	..	..	..
3½	..	..	..	5	6	14	11	8	3	..	..	..	..	..
3¾	..	..	..	0	2	8	17	8	7	1	1	..	..	..
4	..	..	..	2	4	6	14	15	5	8	2	..	..	..
4¼	..	..	..	..	3	4	4	8	12	5	1	1	..	..
4½	..	..	..	..	..	2	7	6	12	9	4	0	1	..
4¾	..	..	..	..	..	0	5	7	6	6	2	0	0	..
5	..	..	..	..	..	1	4	6	8	5	2	2	1	..
5¼	..	..	..	..	..	1	2	6	6	6	5	1	0	..
5½	..	..	..	..	..	..	2	0	5	5	1	0	0	..
5¾	..	..	..	..	..	..	0	2	4	7	1	1	0	..
6	..	..	..	..	..	..	1	..	2	3	0	1	1	..
6¼	..	..	..	..	..	..	..	..	0	0	2	2	1	..
6½	..	..	..	..	..	..	..	..	3	1	6	0	2	..
6¾	..	..	..	..	..	..	..	..	0	0	0	1	0	..
7	..	..	..	..	..	..	..	..	2	2	0	2	0	..
7¼	..	..	..	..	..	..	..	..	..	0	0	3	1	..
7½	..	..	..	..	..	..	..	..	..	0	1	..	..	..
7¾	..	..	..	..	..	..	..	..	..	0	1	..	..	..
8	..	..	..	..	..	..	..	..	..	1	..	..	..	..
10½	..	..	..	..	..	..	..	..	..	..	..	..	..	1

[a] The average fish is older than the exact age given by enough to cause an estimated 75 per cent of the current year's growth.

near Station VII and that immigration is needed to maintain the population.

Tables VII and VIII show the size distributions by ages in the standard-gang samples, the latter for the northeast end of the lake, the former for the remainder. In these tables the effect of net selection is obscured because the size ranges of

TABLE VII. The number of fish of a given age which are of a given weight in a representative sample of whitefish taken in "standard gangs" in parts of Great Slave Lake other than the vicinity of Station VII.

Wt. in lbs.	Age in years[a]																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	23
0	4	18	6	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
¼	1	22	50	89	99	57	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..
½	..	1	..	8	22	61	62	25	2	..	..	..	..	..	..	..	..	..	..	..	..
¾	..	..	..	..	..	23	25	39	6	1	..	..	..	..	..	..	..	..	..	..	..
1	..	..	..	..	..	3	13	21	13	5	1	..	..	..	..	..	..	..	..	..	..
1¼	..	..	..	..	..	..	2	9	18	11	1	..	..	..	..	..	..	..	..	..	..
1½	..	..	..	..	..	..	0	7	14	16	6	2	..	1	..	..	..	..	..	..	..
1¾	..	..	..	..	..	..	2	0	9	22	6	4	..	3	..	..	..	..	..	..	..
2	..	..	..	..	..	..	0	0	3	13	8	3	2	3	1	..	..	..	..	..	..
2¼	..	..	..	..	..	..	1	0	0	3	18	7	3	4	1	..	..	..	..	..	..
2½	..	..	..	..	..	..	..	1	1	5	7	7	5	7	4	2	..	..	..	..	..
2¾	..	..	..	..	..	..	..	..	0	3	5	10	7	5	4	0	1	..	..	..	..
3	..	..	..	..	..	..	..	..	0	1	3	2	11	5	4	2	1	..	..	..	..
3¼	..	..	..	..	..	..	..	..	0	..	1	3	8	10	3	4	0	..	..	..	..
3½	..	..	..	..	..	..	..	..	1	..	..	0	6	16	5	7	4	..	..	..	..
3¾	..	..	..	..	..	..	..	..	..	..	..	0	5	3	9	3	2	..	..	..	..
4	..	..	..	..	..	..	..	..	..	..	..	1	0	1	3	2	2	..	..	..	..
4¼	..	..	..	..	..	..	..	..	..	..	..	..	1	..	2	1	4	2	..	..	..
4½	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	2	1	..	..	..
4¾	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	0	..	..	..
5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0	2	0	..	..	..
5¼	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	0	0	..	..	..
5½	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0	0	0	1	..	..
5¾	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	0	0	0	..	..
6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	1	..	..
6¼	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..
9½	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1

[a] The average fish is older than the exact age given by enough to cause an estimated 29 per cent of the current year's growth.

the fish caught in various meshes overlap. Although these data are scanty, as far as they go they support the ideas expressed above: that whitefish in the north-east part of the lake (i.e. black whitefish) grow the faster; and that the whitefish population there depends on immigration to maintain the observed level of abundance.

Average weights were calculated for each age from Table V and these data were used to plot the solid line shown in Figure 7A. In this graph the average weights were plotted at "ages" 9.42, 10.42, 11.42, etc., on the grounds that the fish had made an average of 42 per cent of their current year's growth up to the time of capture. Similarly the data from Table VII were used to plot the dotted line on Figure 7A. In both cases, only those averages based on at least 20 fish were used.

The two curves represent rate of growth in commercial-fish samples and in standard-gang samples respectively. A comparison of the lower parts of the two curves indicates different growth rates depending on what gear is used for sampling—an absurd conclusion. It seems obvious that the apparent differences really are the result of commercial nets selecting only the largest members of the younger age-groups to a much greater extent than the standard gangs. The

Table VIII. The number of fish of a given age which are of a given weight in a representative sample of whitefish taken in "standard gangs" in the vicinity of Station VII, Great Slave Lake.

Wt. in lbs.	Age in years[a]																	
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20
¼	1	1	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
½	..	..	..	5	2	..	..	..	..	..	..	..	..	..	..	..	..	..
¾	..	..	..	3	2	1	2	..	..	..	..	..	..	..	..	..	..	..
1	..	..	..	1	0	0	2	..	..	..	..	..	..	..	..	..	..	..
1¼	..	..	..	..	1	2	..	..	1	..	..	..	..	..	..	..	..	..
1½	..	..	..	..	..	1	..	3	0	..	..	..	..	..	..	..	..	..
1¾	..	..	..	..	..	..	..	2	0	..	..	..	..	..	..	..	..	..
2	..	..	..	..	..	..	..	1	1	3	..	..	..	..	..	..	..	..
2¼	..	..	..	..	..	..	..	1	2	0	..	1	1	..	..	..	..	..
2½	..	..	..	..	..	..	..	..	3	2	1	1	0	1	..	..	..	..
2¾	..	..	..	..	..	..	..	..	1	1	0	3	1	0	..	..	..	..
3	..	..	..	..	..	..	..	..	..	..	0	4	4	2	..	..	..	..
3¼	..	..	..	..	..	..	..	..	..	..	2	2	1	1	..	..	..	..
3½	..	..	..	..	..	..	..	..	..	..	1	0	1	0	3	..	..	..
3¾	..	..	..	..	..	..	..	..	..	..	0	1	1	0	2	..	..	..
4	..	..	..	..	..	..	..	..	..	..	0	2	0	4	0	..	..	..
4¼	..	..	..	..	..	..	..	..	..	..	1	1	3	0	1	..	..	..
4½	..	..	..	..	..	..	..	..	..	..	0	1	1	2	1	1	..	..
4¾	..	..	..	..	..	..	..	..	..	..	0	1	2	0	1	2	..	..
5	..	..	..	..	..	..	..	..	..	..	1	0	0	1	0	2	2	..
5¼	..	..	..	..	..	..	..	..	..	..	..	0	0	..	2	3	1	..
5½	..	..	..	..	..	..	..	..	..	..	0	1	..	1	1	1	..	..
5¾	..	..	..	..	..	..	..	..	..	..	..	0	..	..	..	0	0	..
6	..	..	..	..	..	..	..	..	..	..	..	0	..	..	..	1	1	..
6¼	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	0	..	1
7¼	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1

a The average fish is older than the exact age given by enough to cause an estimated 28 per cent of the current year's growth.

apparent discrepancy between growth rates in the older fish is attributed to normal variation in what are actually rather small samples of the weights at these ages. The fact that standard-gang samples were taken in water of a shallower average depth than the commercial-fish samples may have had some effect.

The curve shown in 7B is probably a good approximation to the actual growth curve in the population. It follows that part of the growth curve for commercial fish which applies to age 15 and older, and that part of the growth curve for standard-gang fish which applies to those fish from ages 5 to 11. For other ages, it falls below both curves to compensate for net selection—the amount of compensation is of course guesswork. The growth rate of Great Slave Lake fish seems to be slower than that found for most whitefish populations that have been studied.

SOME THEORETICAL CONSIDERATIONS

In an earlier section the annual mortality rate for fish from ages 17 to 22 was found to be 61 per cent. It is again emphasized that this value represents the mortality rate in an unexploited population.

It would be very interesting to know the mortality rate among younger fish, and a rough idea of its magnitude can actually be deduced from Rawson's (1951)

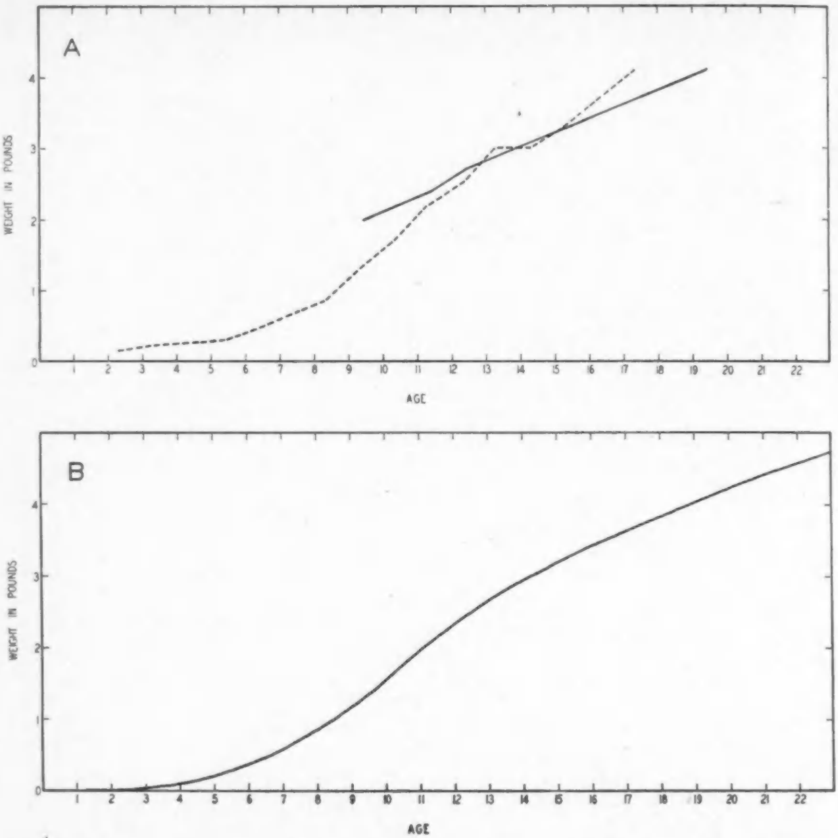

FIGURE 7A. The relationship between age and average weight in samples of Great Slave Lake whitefish.
Dotted line–samples caught in standard gangs
Solid line–samples from commercial catch.
B. Probable approximate age–weight relationship for average Great Slave Lake whitefish.

Figure 6, in which are shown frequency distributions of the lengths of fish caught in each of six mesh sizes. From our Figure 7B the ranges in weight which represent the range of half a year on either side of each age can be determined, hence by use of the length–weight relationship given above (p. 417) the corresponding ranges in length can be calculated. The number of fish which in Rawson's Figure 6 lie within each range in length can be regarded as approximately equivalent to the number of fish of the corresponding age. It is emphasized that only a very rough idea of the number of fish of a given age can be derived in this way, since there is such a large range in the size of fish of any given age, since net selection is an important factor, and since Rawson's Figure 6 is based on disproportionate

numbers of the atypical (because faster growing and predominantly larger) fish from the east end of the lake.

If the logarithms of these estimated numbers are plotted against the corresponding ages, a typical catch curve for each mesh size results, with a more or less straight line in the right limb indicating mortality rates as follows: in 1½-inch mesh catches a rate of 71 per cent for ages 5 to 7; in 2-inch mesh catches a rate of 58 per cent for ages 6 to 7; in 3-inch mesh catches a rate of 64 per cent for ages 8 to 9; in 4-inch mesh catches a rate of 36 per cent for ages 12 to 15; and in combined 5-inch and 5½-inch mesh catches a rate of 36 per cent for ages 12 to 17. The apparent changes in mortality rates with age are not necessarily indicative of real differences, in view of the sources of error listed above. It is probably not safe to conclude any more than that the mortality rates for fish of ages 5 to 16 are not drastically different from those for fish of ages 17 to 22. The data available for the few fish caught in standard-gang samples, where both the age and the mesh size are known, also indicate similar mortality rates for younger fish.

It is instructive to make a series of calculations of the kind shown in Table IX. The first five columns are concerned with the calculation of the average num-

TABLE IX. The number of fish of each age which various assumed annual mortality rates indicate must be present at any given spawning time for every fish that is age 23, and the calculated number of mature eggs which the fish of each age class carry then.

0	1	2	3	4	5	6	7	8	9	10	11
					Av. no.	Hypothesis 1		Hypothesis 2		Hypothesis 3	
Age	% Mature	% Spawning	Av. wt. lbs.	Av. no. of eggs	eggs per fish	No. of fish	No. of eggs	No. of fish	No. of eggs	No. of fish	No. of eggs
0	0	0	..	0	0	25×10⁸	0	41×10⁶	0	26×10⁵	0
1	0	0	..	0	0	99×10⁷	0	16×10⁶	0	18×10⁵	0
2	0	0	..	0	0	39×10⁷	0	65×10⁵	0	13×10⁵	0
3	0	0	..	0	0	15×10⁷	0	26×10⁵	0	88×10⁴	0
4	0	0	..	0	0	59×10⁶	0	10×10⁵	0	61×10⁴	0
5	1.6	0.4	0.30	400	1.6	23×10⁶	36×10⁶	42×10⁴	67×10⁴	43×10⁴	69×10⁴
6	5.2	1.3	0.48	900	11.7	89×10⁵	10×10⁷	17×10⁴	20×10⁵	30×10⁴	35×10⁵
7	12.0	3.0	0.74	1400	42.0	35×10⁵	15×10⁷	66,720	28×10⁵	21×10⁴	88×10⁵
8	30.4	7.6	1.03	2600	197.6	14×10⁵	27×10⁷	26,688	53×10⁵	15×10⁴	29×10⁶
9	58.8	14.7	1.38	4300	632.1	53×10⁴	34×10⁷	13,878	88×10⁵	97,117	61×10⁶
10	78.4	19.6	1.80	7600	1490	21×10⁴	31×10⁷	8,882	13×10⁶	60,213	90×10⁶
11	91.2	22.8	2.19	10,500	2394	80,765	19×10⁷	5,684	14×10⁶	34,923	84×10⁶
12	98.4	24.6	2.53	14,100	3469	31,498	11×10⁷	3,638	13×10⁶	18,859	65×10⁶
13	100	25	2.83	17,200	4300	12,284	53×10⁶	2,328	10×10⁶	9,429	41×10⁶
14	100	25	3.08	19,600	4900	4,791	23×10⁶	1,490	73×10⁵	4,337	21×10⁶
15	100	25	3.33	22,500	5625	1,868	11×10⁶	954	54×10⁵	1,822	10×10⁶
16	100	25	3.54	24,800	6200	729	45×10⁵	610	38×10⁵	729	45×10⁵
17	100	25	3.74	27,000	6750	284	19×10⁵	244	16×10⁵	284	19×10⁵
18	100	25	3.94	29,400	7350	111	81×10⁴	97.7	72×10⁴	111	81×10⁴
19	100	25	4.14	31,800	7950	43.2	34×10⁴	39.1	31×10⁴	43.2	34×10⁴
20	100	25	4.33	33,900	8475	16.9	14×10⁴	15.6	13×10⁴	16.9	14×10⁴
21	100	25	4.50	35,700	8925	6.6	58,679	6.2	55,781	6.6	58,679
22	100	25	4.66	37,400	9350	2.6	23,974	2.5	23,375	2.6	23,974
23	100	25	4.84	39,400	9850	1	9,850	1	9,850	1	9,850

Hypothesis 1—That an annual mortality rate of 61% applies to all ages.
Hypothesis 2—That the annual mortality rate is 60% for ages 1 to 8, 48% for age 9, 36% for ages 10 to 16, and 60% for ages 17 to 23.
Hypothesis 3—That the annual mortality rate is 30% for ages 1 to 8, then increases by 4% per year to 58% at age 15, is 60% at age 16, and 61% for ages 17 to 23.

ber of eggs per fish at each age. Column 1, which shows the percentage of fish of each age that are mature, is derived from the original curve used to get the values shown under "average age" in Table I. Column 2, which shows the percentage of all the fish of a given age which actually lay eggs at any given spawning time, is derived from column 1 on the basis of a previous section (p. 418) where it was shown that about one-half of all the fish are females, and further, that of these about one-half produce mature eggs during any given year. Column 3, which shows the average weight of the fish of each age as of August 14 (the date on which the egg counts were made), is derived from Figure 7B. Column 4, which shows the average egg count in spawning females is derived from Figure 2 by using the value shown in column 3. Column 5, which shows the average number of mature eggs available from all the fish of each age, is calculated by multiplying the values in column 2 by those in column 4.

The remainder of the table shows the results of calculations based on three different assumptions regarding mortality rate. They are intended to serve as examples of the many similar assumptions that could be made. For each assumption the first column (i.e. columns 6, 8 and 10) shows the number of fish that must survive to each age for every fish that survives to age 23 at the assumed mortality rates. The population is considered at spawning time when each fish is approximately half a year older than it was when it was exactly the age indicated. As an example of the calculations required, consider assumption 1. By definition there is only one age-23 fish and it is actually 23½ years old, and by definition the mortality rate at exactly age 23 is 61 per cent which is the rate from the time a fish is 22½ years old until the time it is 23½ years old. Since at spawning time the fish listed as age 22 are actually about 22½ years old and those listed as age 23 are actually about 23½ years old, the mortality rate that is assumed to apply to fish exactly 23 years old (i.e. 61 per cent) can be regarded as the rate acting to reduce the number of age-22 fish to the number of age 23; stating it another way, only 39 per cent of the fish listed as age 22 at one spawning time survive to be listed as age 23 exactly one year later. Obviously there must be $1 \times \frac{100}{39} = 2.564{,}103$ age-22 fish for every one age-23 fish. Similarly, there must be $2.564{,}103 \times \frac{100}{39} = 6.574{,}622$ age-21 fish and so on. To conserve space, fewer significant figures are shown than were used in the actual calculations. The other column (columns 7, 9 and 11) under each assumption shows the calculated number of eggs available for spawning, and is found by multiplying the average number of eggs per fish by the calculated number of fish.

Hypothesis 1 visualizes a population of 2,500,000,000 fish at age 0 (i.e. when half a year old). Since the calculations show that such a theoretical population can produce only 1,600,000,000 mature eggs per year (found by summation of the second column under assumption 1), this assumption is untenable. Obviously, at some time earlier than age 17 the annual mortality rate of Great Slave Lake whitefish must be less than 61 per cent. Calculations similar to those shown for

assumption 1, except that a mortality rate of 58 per cent is used, give 460,000,000 fish of age 0 for a population that can lay 590,000,000 eggs. While this situation is theoretically possible, it seems unlikely, because the loss of only 22 per cent from eggs to the fish one year later includes eggs which are retained in the ovary and eggs that are spawned but not fertilized as well as the actual mortality (first as fertile eggs, then as young fish) during the year.

Hypothesis 2—which takes the mortality rates calculated from Rawson's Figure 6 more or less at their face value—is that the mortality rate is constant at one level, drops abruptly to another level then returns to the original level. It visualizes 41,000,000 fish after one year from 88,000,000 eggs available for spawning. In this case the "mortality rate" for age 0 (i.e. the average rate of loss from the instant the female extrudes them until one year later) must be only 53 per cent, which is theoretically possible although hard to imagine. Moreover, abrupt changes in mortality rate of the kind visualized by hypothesis 2 are not characteristic of mortality rates in most animal populations where this factor has been studied in detail.

Hypothesis 3, which is more nearly characteristic of mortality rates in other animal populations, visualizes a rate which remains constant at a lower level from age 0 to age 8, then increases gradually to age 17 after which it remains constant. It visualizes 2,600,000 fish after one year from 420,000,000 eggs available for spawning. This involves a "mortality rate" of 99.4 per cent at age 0, which is in marked contrast to the mortality rate of 30 per cent assumed at age 1. If the rate at age 1 is assumed to be 60 per cent, the "mortality rate" at age 0 becomes 99 per cent, in which case the contrast is less pronounced. Other similar assumptions can be made, for instance: an assumed gradual increase from a mortality rate of 30 per cent at age 1 to 61 per cent at age 17 then remaining constant implies 13,000,000 fish after one year from 610,000,000 eggs, which involves a "mortality rate" of 98 per cent for age 0; or an assumed rate of 50 per cent for ages 1 to 11 with a gradual increase to 61 per cent at age 17 then remaining constant implies 91,000,000 fish after one year from 630,000,000 eggs, which involves a "mortality rate" of 85 per cent for age 0.

These hypotheses by no means exhaust the possibilities. They do show roughly the outlines of what seems reasonable. It appears obvious that the mortality rate found to apply to the older fish cannot be regarded as applying to all ages, and that at some earlier age there must have been a lower rate. If it is assumed that the lower rate of mortality occurs between ages 8 and 16, then, although the calculations indicate a smaller population at age 0, they also indicate fewer eggs, so that a drastically lower mortality rate must be assumed if the "mortality rate" at age 0 is to be regarded as appreciably greater than any given in Table IX. It seems unlikely that the mortality rate could be drastically lower for any ages between 8 and 16, because that would involve a too abrupt change in mortality rate and especially because a rate that was appreciably less than 30 per cent for fish of any of the ages 10 to 17 would be inconsistent with the shape of the dome shown in Figure 6A. A mortality rate appreciably less than 30 per

cent for fish from age 5 to 9 seems too inconsistent with rates calculated from Rawson's Figure 6. A very low rate among fish of ages 1 to 4 would seem unreasonable if a high value is assumed for age 0.

It is unnecessary to decide which hypothesis is most reasonable in order to see that there are certain principles involved which lead to the following conclusions regarding Great Slave Lake whitefish:

1. An annual mortality rate of 61 per cent between ages 17 and 22 is consistent with all other available facts.

2. It is unnecessary to postulate a high proportion of unfertilized eggs, or a tremendous loss among fertilized eggs, or a drastic mortality rate among fry and young fish to explain the fact that only one pair of fish results from many thousands of eggs.

3. For any hypothesis that seems reasonable, most of the spawn is produced by fish which are too small to be fully vulnerable to the gear now used, and approximately one-half of it is produced by fish that are for all practical purposes too small to be taken at all. In other words it seems unlikely that a fishery such as the present one, even if it became more intensive, would interfere with adequate spawning.

4. For any hypothesis that seems reasonable it is seen that a given year-class would have its maximum bulk at some age at which individual fish are much too small to be useful as commercial fish. Each year-class whose members are big enough to be caught by a 5½-inch mesh represents a crop from which the maximum yield could be gained by harvesting it immediately, since more weight is being lost by natural mortality than is being added by growth. Therefore, a more intensive fishery would be expected to produce a greater sustained annual yield.

The values for maturity, sex ratio, frequency of spawning and egg counts, all of which enter into the calculations of Table IX, are admittedly based on a minimum of data. It might, therefore, be argued that these conclusions are unreliable. However it can easily be shown that even considerably different values would not change these conclusions.

SUMMARY

1. A population of whitefish was observed in the unexploited condition and observations were continued during four years of commercial fishing. Ages were determined for 6,571 fish.

2. An equation was found for the length–weight relationship.

3. Fish of both sexes mature anytime between age 4 and age 13, when they are between 7 and 18 inches long and weigh between 0.3 and 2.8 pounds.

4. There is evidence of a race of "dwarf whitefish", probably rarely encountered.

5. The sex ratio is approximately 1:1.

6. Only about one-half of the mature females spawn each year.

7. The relationship between the size of the female and the number of eggs she produces is shown graphically.

8. There is practically no growth except from the middle of June until the

end of September, and almost one-half of all the growth for the year is made during the first half of August.

9. All year-classes seem to be of equal strength.

10. Each year 61 per cent of the whitefish of ages 17 to 22 die from "natural causes". Theoretical considerations indicate a slightly lower mortality rate among younger fish.

11. Commercial fishing for four years produced no measurable change in total annual mortality rate.

12. There is evidence that the whitefish population in the northeast part of the lake depends on immigration to maintain itself.

13. Only the largest fish are captured from many of the age-groups which contribute to the commercial fishery, so that a distorted idea of growth rate would result from the uncritical use of the relationship between size and age.

14. They grow slower than most populations of whitefish that have been studied. The rate of growth is illustrated graphically.

15. Fish in the northeast part of the lake—so called "black whitefish"—grow appreciably faster than those from other parts.

16. Moderate mortality rates acting at each age are sufficient to account for all the losses that obviously must occur when thousands of eggs are produced for every adult fish that results.

17. Most of the spawning is done by fish that are too small to be fully vulnerable to the commercial fishing gear used.

18. A more intensive fishery would probably increase the sustained annual yield of whitefish.

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An Economic Approach to the Optimum Utilization of Fishery Resources

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(Received for publication February 2, 1953)

INTRODUCTION

The control and regulation of the fishing industry by legislation and governmental administration is now of long standing. Many of the world's major fisheries have been placed under some kind or other of "conservational" control. The regulations that have been developed to protect the fishery from overuse are in many cases so extensive in scope and intensive in degree that they greatly exceed those which are applied to any other industry. These regulations and restrictions have developed from the conviction that the fishery resource is especially liable to depletion through too intensive or improper use. This conviction is very widely held and, despite the fact that fishery regulations are, in many countries, extraordinarily severe, there has been remarkably little opposition to them, even on the part of the fishermen affected. There is, I think, some considerable tendency, in administrative quarters at least, to regard "conservation" as a desirable objective without any satisfactory definition of its meaning and without sufficient study of the means whereby the ends are to be achieved.

Most of the studies of fisheries conservation have, up to this point, been undertaken by biologists. On the face of it, conservation appears to be a biological problem, and natural scientists have explored its intricacies with considerable vigour and some success. It soon becomes evident, however, that the problem runs far beyond biological factors. The purpose of a fishery is the *human* use of a source of food. Fishing is carried on by human beings for human purposes. Any successful evaluation of the aims and methods of fishery regulations must necessarily involve consideration from the side of the so-called *social* sciences as well as the natural ones. As O. E. Sette has put it: ". . . the method of conserving a commercial fishery involves social, economic, and political considerations and lies in the field of political economy."[1]

The purpose of this paper is to approach the problems of optimum human utilization of fishery resources from the side of one of the social sciences—economics. I believe that an application of some of the standard devices of economic

[1]O.E. Sette, *Studies on the Pacific Pilchard or Sardine,* U.S. Fish and Wildlife Service, Special Scientific Report No. 19, (1943), p. 4. Cf. also, E. S. Russel, *The Overfishing Problem*, p. 94.

J. Fish. Res. Bd. Can., 10(7), 1953.
Printed in Canada.

theory can help to clarify the objectives of conservation and contribute to a better evaluation of control measures.

An apology is perhaps necessary. This paper is written for a mixed audience so far as economic theory is concerned. There will perhaps be those who are thoroughly familiar with the devices that are employed in the following pages and, to them, some of the explanations and proofs given will be exasperatingly elementary. Others may have had no formal training in modern economic theory and for them it is necessary to include sufficient explanation so that the argument may be followed. I have tried to solve this dilemma by including only the barest amount of explanation necessary to complete the reasoning without taking anything for granted. I am afraid that the result is neither fish, flesh nor fowl, but perhaps it will nevertheless be a synthetic protein with some food value, and not entirely unpalatable at that.

DETERMINATION OF THE ECONOMIC OPTIMUM

Definition of the Optimum

From the economic viewpoint, the principal neglect in most discussions of fishery theory is the factor of cost. Although this has sometimes been mentioned, and occasionally with considerable insight,[2] no satisfactory analysis of this side of the question and its relation to the production side yet exists. Practically every productive activity incurs certain costs in making its output. It is obvious, for example, that if we are to determine the worth or contribution of a steel smelter we must first deduct the value of the coal consumed in producing its product. So it is with every productive enterprise—the measure of its own contribution to human economic welfare is determined by its *net* output, after the costs of the factors necessary to that output's production have been deducted. We can then define the economic objective of a commercial fishery as the achievement of the *maximum net economic yield.* The level of fishing effort which achieves this maximum will be described as the "optimum degree of fishing".

A qualification is at once necessary. As Beverton has pointed out, the economic optimum is not necessarily the *human* optimum. The latter involves social, psychological and political considerations as well as economic ones.[3] Under certain circumstances we may well prefer to have an economically "inefficient" fishery if the other effects of organizing the fishery along economically optimum lines are politically difficult or socially undesirable. This may, of course, be a rational decision, as long as we know what we are doing. If we can estimate the degree of departure from the optimum, the costs of that departure, and other relevant facts, we can still make a rational choice in the matter. Consequently,

[2]See especially R. A. Nesbit, *Fishery Management*, U.S. Fish and Wildlife Service, Special Report, No. 18 (1943); and R. J. H. Beverton, "Some Observations on the Principles and Methods of Fishery Regulations" (mimeo'd), a paper read at the General Meeting of The International Council for the Exploration of the Sea, Copenhagen, 1952.

[3]*Ibid.* This point was also emphasized to me by W. E. Ricker in correspondence on a preliminary draft of this paper.

the burden of this paper is not that the achievement of maximum net economic yield is an unalterable and indisputable objective for a fishery, but that we must know what it is and where it is, in order to make *any* objective a rationally determined one.

Determination of the Optimum

The basic economic problem we must attempt to solve is to find the optimum degree of exploitation of a fishery. Both primitive factors in this problem—the catch of fish and the costs of fishing—are functions of the amount of fishing effort, so our problem is to determine that amount of effort which will maximize the difference between landings (measured in money terms) and costs. This optimum is, of course, dependent on the nature and shape of the functions relating cost with effort and landings with effort.

The simplest expression of the landings function can be made on the assumption that all factors other than fishing effort are impounded in *ceteris paribus*. The most important feature of this assumption is that it means that, in this simple case, the population of fish is not affected by fishing effort. This is not an entirely unrealistic case although it is one that would, in practice, excite little practical concern from the standpoint of conservation. If we fix our attention on this simple case however, we can see the operation of one of the most important factors in the problem—the "law of diminishing returns".

In Figure 1, a standard "production function" of economic theory is drawn (L) which embodies the law of diminishing returns. As fishing effort is increased,

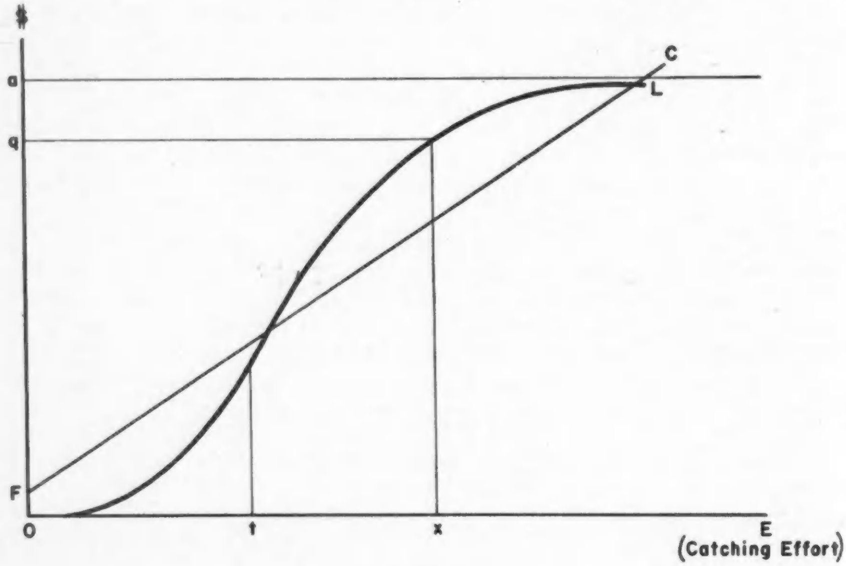

Figure 1

all other factors (including population) remaining constant, the resulting landings grow in the manner described by the curve. When the quantity of effort is very small, the ratio of effort to other productive factors (such as population) is also small, and an increase in effort would raise landings *at an increasing rate*. A practical situation may be visualized where an increase in the number of boats would enable quicker and more effective search for the fish, thereby increasing the fishing productivity of all units. This region is probably very small in most fisheries and non-existent for some. The law of diminishing returns applies to the area beyond the inflection point of the curve (Effort = Ot). As the ratio of fishing effort to other factors of production grows, landings continue to increase but at a diminishing rate. Each additional unit of effort is less and less productive because it has less (on the average) of the other factors (e.g., population) to work with. The production function under such circumstances approaches an asymptote at Oa which represents the maximum sustained physical yield that can be derived from the fishery. This is not the maximum net economic yield because the costs of producing the units close to Oa would obviously be very high. The problem is to find what effort will constitute the economically optimum fishing intensity.

Before this is done, it may be worthwhile to "prove" that a fishery will, in normal circumstances, be subject to the law of diminishing returns as described. Let us envisage a fishery operating over a geographical area in which the relationship between landings and effort is linear and the law of diminishing returns is not operative. This is represented in Figure 2, where the fishing area

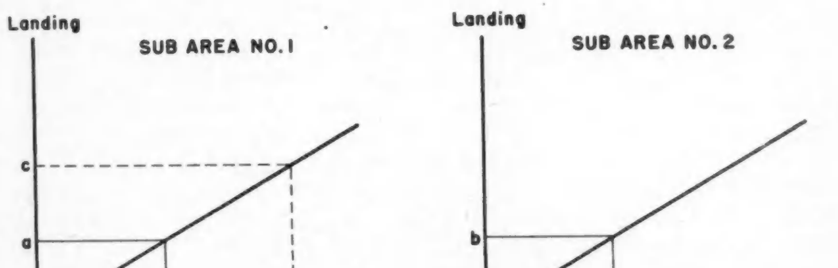

FIGURE 2

(assumed to be homogeneous in everything but position) is divided into any two sub-areas. A linear production function is assumed to be operative on each area, as shown. Any amount of fishing effort expended could do just as well by concentrating in one sub-area as by using the whole. That is, if total fishing effort is put half in sub-area 1 and half in sub-area 2, Ox = O′y. Total fishing effort

used = Ox + O′y, so total landings will be Oa + O′b. If all the effort is concentrated on sub-area 1, the total landings will be the same:

$$Oz = Ox + O'y$$
$$Oc = Oa + O'b$$

Thus there is no point in using both areas if there is any cost advantage *at all* in using only one. Sub-area 1 can now be divided and a similar proposition proved—thus one arrives at the conclusion that if the law of diminishing returns does not apply, all the world's fish can be caught in one bay merely by increasing the catching effort. This *reductio ad absurdum* forces one to the conclusion that, even if the fishery is such that population is unaffected by fishing, it would be exploited in the most accessible area to the point of diminishing returns before expanding to any additional area. Therefore any actual fishery may be presumed to operate in an area of diminishing returns—beyond Ot in Figure 1.

It should be noted that those who are unconvinced by this proof of the "law of diminishing returns" or who feel that it is not applicable to the fishing industry need not fear that the basic argument of this paper is based on it. All that is necessary is that we grant that the relationship between effort and landings is as shown by the curve L in Figure 1. We may assume that this is due either to the law of diminishing returns, or to the effect of fishing effort on population, or to some combination of the two. In any case, the formal determination of the optimum described in the following pages will be the same, and the reader can determine for himself, in respect of whatever fishery he has in mind, the relative importance of the factors which cause the production function to be non-linear.

The point of maximum net economic yield may be derived for this case if we can add the cost side of the problem. Total cost is composed of two parts: (*a*) The cost of fixed facilities such as wharves, harbours, breakwaters, etc., which, except in a very primitive fishery, must be incurred before any direct fishing effort is made and which, within limits, is independent of the amount of that effort. This is designated as the "fixed cost" of the fishery and is the quantity OF in Figure 1. (*b*) The "variable cost" consists of such items as boats, fuel, nets, bait, food, etc., which are incurred directly as a result of fishing effort. On the assumption that variable costs *per unit* are constant, regardless of the amount of effort (i.e., that the prices of variable cost factors are unaffected by the amount employed),[4] the functional relationship between total cost and fishing effort is a straight line, C, in Figure 1. An element of variable cost included in C is the remuneration of the fishermen for their own labour. This factor is valued at the rate that is paid for other labour of comparable skill and difficulty in the community under consideration, assuming that no great difficulty exists in finding employment.

The net economic yield of the fishery which is represented by the landings and cost functions of Figure 1 is the vertical distance between L and C. This

[4]This assumption is reasonable for a particular fishery, since it rarely uses a major proportion of the total production of these factors; but even if this were not the case, the general conclusion we shall draw would be the same.

distance is at a maximum where the slope of the landings function is equal to the slope of the cost function, or where

$$\frac{dL}{dE} = \frac{dC}{dE}.$$

In the language of economic theory, the optimum level of production is where "marginal production" equals "marginal cost". With the functions as drawn in Figure 1, the optimum level of fishing effort is Ox and the catch obtained at the optimum is Oq. As one would expect, *the economic optimum is at a level of fishing intensity somewhat less than that which would produce the maximum physical landing*, even when the latter is a quantity that could be indefinitely sustained.

The definition of the optimum remains the same if we release the assumption that population is unimpaired by fishing. The landings function then rises even more slowly after the point of inflection, and the point of optimum is at a lower effort than before, but it is still defined by the equation of marginal production with marginal cost.

A slight revision in the presentation will enable some further problems to be attacked. Let us drop the assumption that there is a region in which landings will increase at an increasing rate as effort is expanded. The catch per unit of effort may now be represented as a simple function of the amount of effort. This we may call the average-production function–labelled AL in Figure 3. This is

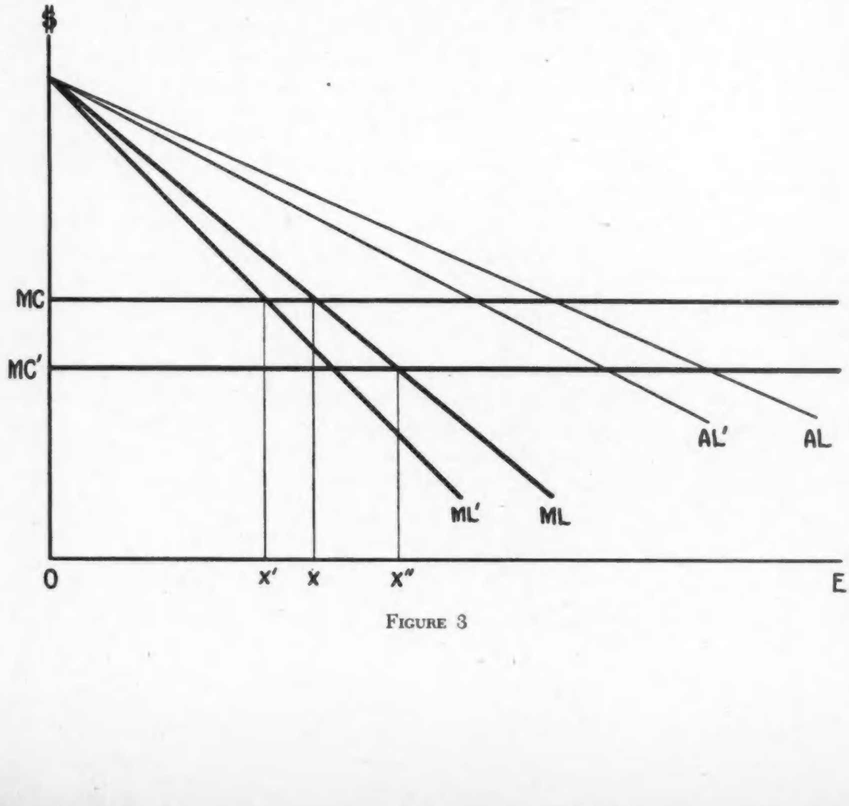

FIGURE 3

drawn as a straight line for simplicity's sake but it need not be so.[5] This simplification will not affect the argument however.

Similarly, the first derivative of the total-landings function may be drawn, and this too will be a straight line if average production is linear. This function is labelled ML, for it is the "marginal production" or "marginal landing"—the change in total production which results from an infinitesimal change in fishing effort. Under the given conditions, the relation between ML and AL will be that ML bisects the horizontal distance from the ordinate to AL; that is, the marginal production will fall twice as rapidly as the average production.[6]

The position of optimum economic yield may now be defined again. Marginal costs (the change in total cost resulting from a small change in effort) are constant in our analysis thus far, under the assumption that the prices of variable factors of production are not affected by the quantity of them purchased by the fishing industry. Thus the constant quantity OMC in Figure 3 represents the marginal cost of fishing effort to the fishery. The optimum is with effort equal to Ox, where MC and ML are equal. At any point to the left of Ox, the net yield of the fishery could be increased by greater effort, for each addition to effort would bring a greater addition to total (money) landings (ML) than to total costs (MC). At any point to the right of Ox, the net yield of the fishery could be increased by contraction of effort, for such a contraction would bring a greater reduction of total costs (MC) than of total receipts (ML).

We can now see that the effect of the impairment of a population by fishing is to increase the rate of fall of the average landing and marginal landing—as shown by the functions AL′ and ML′ in Figure 3. The optimum output will be at a point of lower effort (Ox′) and lower total output, the amount of the difference being dependent on the extent to which the population is impaired by fishing. The following general conclusion may therefore be drawn: *the greater the*

[5]In fact, if total landings approach an asymptote as in Figure 1, average landings would approach zero as an asymptote in Figure 3.

[6]The proof, in geometric terms, is as follows: In Figure 4, linear average-landing and marginal-landing curves are drawn. Let Op be any quantity of effort and Oq the corresponding average-landing per unit of effort. Then,

Total landings = area Oqbp

Total landings may also be expressed as the sum of all the incremental landings ascribable to successive units of effort (marginal landings) from zero effort. Therefore,

Total landings = area Oasp
Since Oqbp = Oasp,
Δaqr = Δrbs

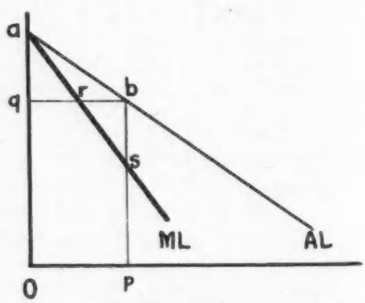

FIGURE 4

Since also, these are right triangles and $\angle$ arq = $\angle$ brs, qr = rb. This holds only for a linear average-landing function.

reduction in fish population that results from fishing, the lower will be the optimum fishing effort.

Figure 3 can also be used to show the effect of a change in fish prices on the point of optimum fishing effort. A fall in fish prices is a fall in the per-unit money value of landings and may be represented by the movement of the average production curve from AL to AL′. The new point of optimum fishing effort, where the new marginal landing (ML′) is equal to the marginal cost (OMC) is at a lower intensity of effort (Ox′). We may therefore conclude: *a fall in the price of fish will lower the point of optimum fishing effort and an increase in price will raise it.*

A change in fishing costs may similarly be analysed. If the average cost of the variable factors of production is reduced, this means a fall in the marginal cost of fishing effort, represented in Figure 3 by a fall in marginal costs from OMC to OMC′. The optimum fishing intensity is now at a higher level than previously, Ox″ as compared with Ox (using ML as the unchanged marginal-landings function). We may therefore conclude: *a decrease in the price that must be paid for fishing gear and supplies will raise the optimum fishing effort, an increase in such prices will lower the optimum fishing effort.*

WHY A FISHING GROUND IS OVEREXPLOITED

The conclusions deduced in the preceding section are of a commonsense nature and I do not imagine that they will be found to be novel by anyone who has studied the fishing industry even without the analytical tools of economic theory. However, the devices which were employed above may help us to approach one of the most vexing questions in the fishery. The danger of overexploitation of fishing grounds is of almost universal concern. Almost every fishery, no matter how prolific, appears to be exposed to this danger. Yet this cannot be owing to the small reproductive ability of fish species, for most of them possess fabulous reproductive powers. It is for this reason that I designate the problem as one of "overexploitation" rather than "depletion" as it is frequently described in the current literature. The great reproductive ability of most species that are commercially fished makes their extinction by man a virtual impossibility. Yet it also seems likely that a fishery of any appreciable size will *reduce* the fish population. If we assume that the species was in ecological equilibrium at a certain population level before fishing began, the development of a commercial fishery constitutes the arrival of a new predator, and for this reason the population equilibrium will be at a lower level. This simple statement must, of course, be qualified to the extent that there may be relationships of predation among commercially exploited populations and to the extent that man may significantly alter the species' physical environment. The problem however is, fundamentally, not one of "depleting" the fish population, it is that of fishing it beyond the point of maximum net economic yield, the effect of fishing on the species population being *one* of the factors taken into consideration.

The argument of the following few pages is that the overexploitation of fishing grounds which is so widely encountered is due to powerful economic

forces. The fundamental cause of this overexploitation is the fact that fishing grounds are, in most cases, the *common property* of all who may wish to use them.

Let us consider two geographically separate fishing grounds. What allocation of fishing effort between the two grounds will maximize the total net yield? In Figure 5 these two grounds have been represented by the average-product and marginal-product functions AP_1 and MP_1 for Ground No. 1, and AP_2 and MP_2

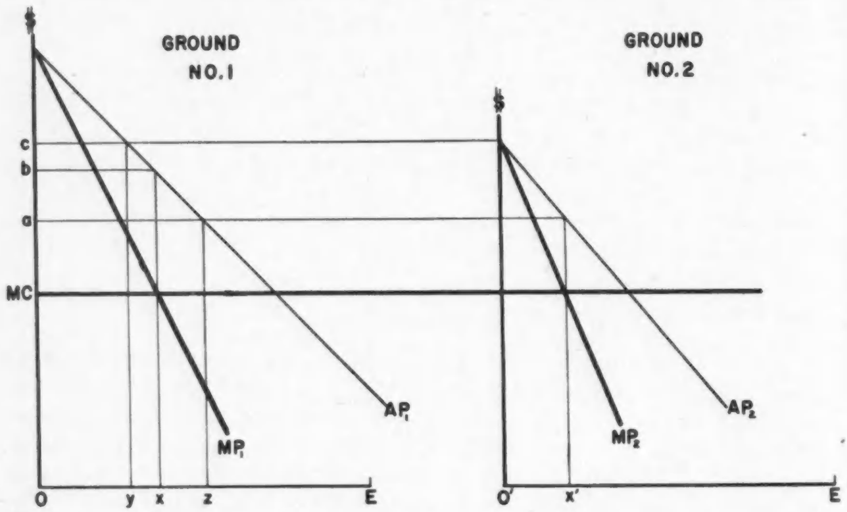

FIGURE 5

for Ground No. 2. As the diagram indicates, equal quantities of effort will yield less on Ground No. 2 than on Ground No. 1. This may be due only to the superior location of the latter, or it may be the result of any factor or group of factors that makes any one fishing ground more "productive" than another. The theorem I shall attempt to illustrate is perfectly general.

If OMC is the ruling price of variable factors of production in the fishing industry (or the "marginal cost of effort"), we already know from the preceding argument that the net economic yield on Ground No. 1 will be maximized when the fishing effort applied to the ground equals Ox. Similarly O′x′ applied to Ground No. 2 is the optimum there. If Ox + O′x′ is the total amount of fishing effort applied to both grounds, it can be seen that the distribution of it as shown is the one that will produce the largest total catch of fish from both grounds. If, for example, some of the O′x′ effort were shifted from Ground No. 2 to Ground No. 1 the addition it would make to the total product of No. 1 when added to Ox would be less than the production which would be lost when that effort is taken from No. 2. That is, if effort is shifted from Ground No. 2 to Ground No. 1,

$$MP_2 > MP_1$$

and since MP_2 is the amount lost on No. 2 while MP_1 is the amount gained on No. 1, the aggregate total production of both grounds is reduced by this shift of effort. Similarly, it can be shown that the aggregate is reduced by any shift of fishing effort from Ground No. 1 to Ground No. 2.

The optimum utilization of each fishing ground taken separately then, produces the optimum allocation of effort among all grounds taken together. *The optimum geographic distribution of fishing effort is such that the marginal productivity of effort is equal in all areas.*

Such a rational allocation of effort can be made by a farmer in respect of his various fields, and if each farmer equated marginal productivity with marginal cost on his whole farm in order to maximize its net income, the farming land of the whole community would be utilized to the different degrees of intensity appropriate to each part. This is, of course, an ideal picture even for farming, but the main point I wish to make is that such a rational allocation of human productive effort is a total impossibility for most fisheries. The great difference between farming and fishing is that the individual farmer possesses legally sanctioned control over a portion of the natural resource while the fisherman has none.[7] Farmer X could not come and cut Farmer Y's grain a day or so before he intended to mow it himself. He could not slaughter the other's cattle before Y intended to do so. These items are given the status of private property. The fisherman however does not possess private property in the resource. Except in a few minor cases like oyster culture, the resource is open to all who wish to take it, and the competition that exists among the various fishermen results in a misallocation of fishing effort, to the consequent inevitable overexploitation of the richer or more accessible grounds.

We can see the operation of this in Figure 5. We have already determined the optimum allocation of effort to be Ox on Ground No. 1 and O′x′ on Ground No. 2. Now, take a fisherman about to start from port and deciding whether to go to No. 1 or No. 2. What is the factor which determines that decision? It is not the relative *marginal* productivities of the two grounds but their *average* productivities. The fisherman does not ask what allocation of effort will maximize the aggregate production of the fishing fleet but what action will give him, individually, the greater yield. In the case shown, he is clearly not indifferent as between Ground No. 1 and Ground No. 2. If he fished on No. 2 his average production per unit of effort would be Oa and his total catch would be Effort $\times$ Oa, but on No. 1 his average production would be higher, Ob, and his total catch, Effort $\times$ Ob, consequently higher also. A fisherman would therefore be foolish to fish on Ground No. 2, so the optimum allocation of fishing effort is not, in actuality, a position that will be achieved as a result of the individual actions of fishermen. In the illustration shown, Ground No. 2 would not be used at all until the average production per unit of effort on Ground No. 1 were reduced to Oc. Ground No. 2

[7]This fact is well emphasized in Harden F. Taylor, *Survey of Marine Fisheries of North Carolina* (Chapel Hill, 1951).

would not be fished with the optimum quantity of effort until Oz of effort was expended on No. 1, and this of course, exceeds the optimum amount of effort for Ground No. 1.

We therefore come to this conclusion: *when a fishery is carried out on grounds of different productivity the richer (or nearer) grounds will be over-fished.* The effect of this is that the net economic yield that could have been obtained from the richer grounds is dissipated through misallocation of fishing effort.

By making our illustration a little more general it can be shown that the final result of this process is the dissipation of the whole of the net economic yield. Let us suppose that there is a continuous gradation of fishing grounds in respect of their productivity. The simplest case that can be envisaged is where the grounds are homogeneous in all relevant factors but, as they must, differ in location. If we measure fishing effort in terms of number of days absent from port or some such quantity, it is apparent that, other things being equal, the yield of a ground will vary inversely with its distance from port. This situation is represented in Figure 6 on three charts. Ground No. 1 is the nearest, Ground

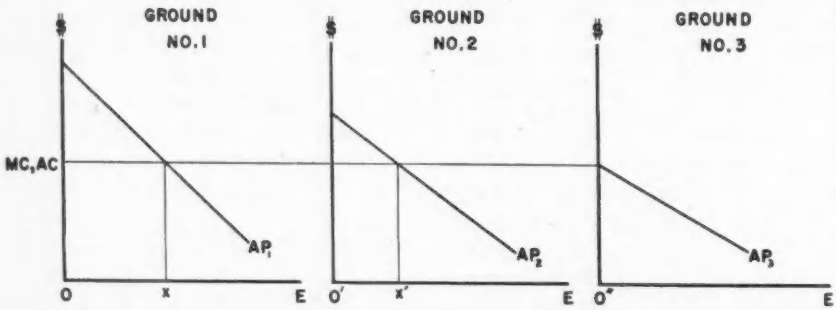

FIGURE 6

No. 3 the farthest of those being fished. Ground No. 2 is one of intermediate location. We can imagine an infinite number of diagrams between No. 1 and No. 3, representing the infinite number of locations that would exist if location is to be regarded as a matter of infinite gradation.

In Figure 6, Ground No. 3 is the most distant area it pays to fish. That is, fishing in this area yields no more than cost, as we have been measuring it in this paper. Ground No. 3 is, in fact, on the margin of cultivation and it is probably most realistic to regard it as being fished only intermittently, and what we have to say about it will be in the form of what would be the case if it were regularly utilized to a very small extent.

It will be remembered that we have been assuming that the cost per unit of fishing effort is constant. (This is a simplifying assumption that does not alter the conclusions reached.) This means that the marginal cost of effort (the addi-

tion to total cost that results from the addition of a small unit of effort) and the average per-unit cost of (variable) effort are the same. They are both represented as being constant by the horizontal line drawn through all three units of Figure 6. If Ground No. 3 is on the margin of use, it is the one on which average cost and average production are equal, and, since

$$\text{Total cost} = AC \,.\, E$$
$$\text{and Total production} = AP_3 \,.\, E,$$

total cost and total production will also be equal under such circumstances. We have allowed as part of costs the income a fisherman could make by working in an alternative occupation, so we may say that the marginal ground—No. 3—yields such income but no more. (This conclusion will be further modified in a moment.)

This is, of course, also the case with marginal agricultural land, but in agriculture there is nothing to prevent the intra-marginal land from showing a net economic yield. In the fishery, however, this yield is dissipated. In Figure 6, no fisherman will proceed to Ground No. 2 until the average productivity of No. 1 has fallen to the level of No. 2 and no one will contemplate fishing on No. 3 until the average productivity of Nos. 1 and 2 have fallen to its level. Thus if the ground on the margin of cultivation is one where average production equals average cost and total production therefore equals total cost and there is no net yield, then that is also the case with all intra-marginal areas as well. Thus in the illustration shown in Figure 6, Ground 3 is on the margin of use, No. 2 has O′x′ of effort devoted to its exploitation, and No. 1 has Ox of effort in use. In all cases $AP = AC$ and there is no net yield.

If we translate this illustration back into the total-production and total-cost functions employed in Figure 1 we can perhaps make the matter clearer and, in addition, extend the analysis. In Figure 7 the situation is redrawn in terms of total-cost and total-production curves, C and L. The point of optimum exploitation is where the vertical distance between these two is maximized. This is where $\frac{dC}{dE} = \frac{dL}{dE}$ or where "marginal cost" equals "marginal production". In the figure as drawn, the optimum is at effort Ox and total production Oq. If the ground depicted is overexploited to the point where no net yield exists, this will be where total cost equals total production; in Figure 7 with Og of effort and Ot of production. At this point fishermen are earning labour incomes equivalent to those that could be obtained from other industries and no more, but the competition among them for fish may not end there. They may expand their efforts even beyond Og. This is equivalent to revaluing their own labour. Fishermen accept incomes lower than those of other employment. This means that a major element of variable cost is valued at a lower per-unit sum. The slope of the total-cost function, C, represents the average variable cost, so the slope of this function is lowered as shown, to C′ and C″, fishing effort expands to g, h, i, and so on, with the fisherman getting a smaller and smaller reward for his work.

This, I think, is what accounts for the relatively low incomes of fishermen which are almost everywhere experienced. The form of competition which exists

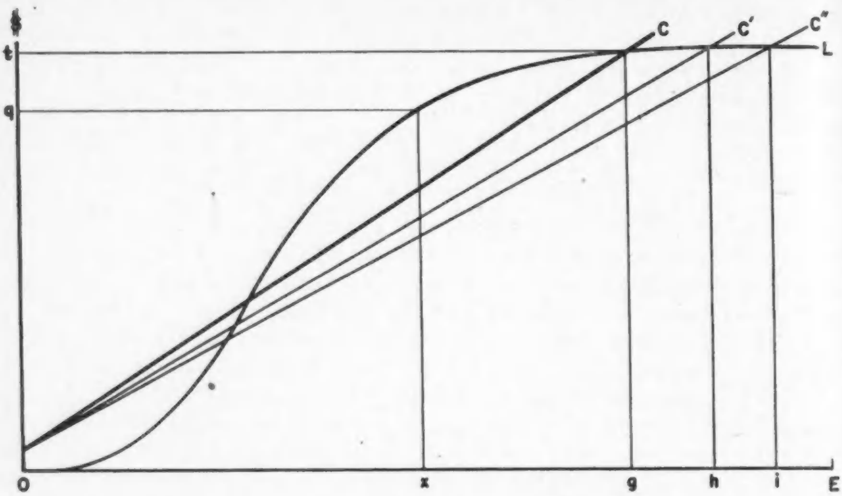

FIGURE 7

in fisheries for open resources not only dissipates any net yield that might have been attained, but goes farther and reduces the straight labour income of fishermen below that of other occupations. The immobility of fishermen, their attachment to their local communities and to their occupations, prevents an equilibrium of labour income from being established with that of other industries, and the result is that even in fisheries where the resource is rich, the fishermen are poor.

(There are some fisheries in which the expansion of fishing effort will after a point, reduce the total landing of fish rather than approaching an asymptote as in Figure 7. This is the case especially where the average size of the fish is substantially reduced by fishing. This case is depicted by the landings function, L, in Figure 8, which reaches a maximum and then declines. The expansion of fishing effort to g, h, i, and so on, results in landings of t, u, v and so on. This case is not fundamentally different from the former one.)

PRACTICAL MANAGEMENT POLICY

The subject of "fisheries management" has received considerable attention in recent years, particularly from biologists. It has generally been recognized that the objectives of fisheries management are economic in nature, but no coherent analysis of these objectives yet exists. If the theory of optimum exploitation put forward in the preceding sections of this paper has any empirical validity, it should aid us in coming to grips with the problem of formulating a practical policy of fisheries management. I believe that it can do this although its principal conclusion is that the implementation of such a policy is enormously difficult in the case of open sea fisheries. However, our theory can, at the very least, explain the lack of success achieved by management policy to date. It will not be possible,

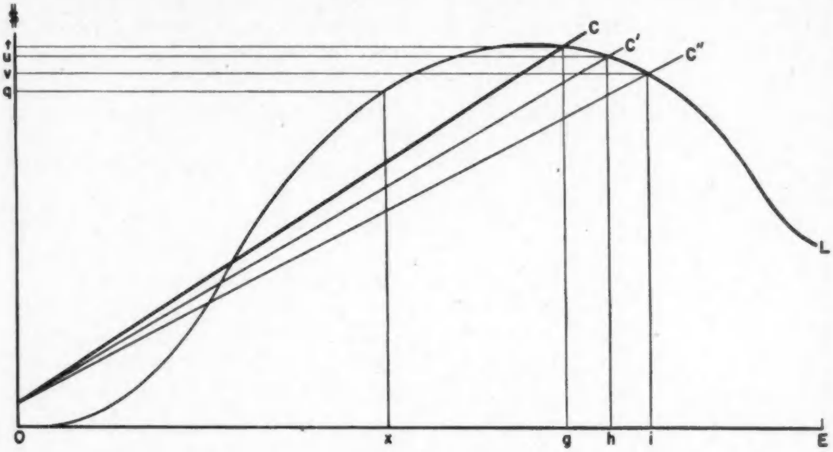

FIGURE 8

within the scope of this paper, to examine all types of management methods in the abstract, much less to study exhaustively the practical cases with which world fisheries abound. Rather the purpose of the following few pages is to apply the theoretical presentation of the preceding sections to two major types of fisheries management, in a very preliminary fashion.

The catch-limit method has recently received a great deal of favourable consideration, owing primarily I believe to the apparent success of the Pacific halibut programme. Although it is by no means clear that the limitation of catch imposed upon the fishery is the most important factor accounting for the rise in the halibut population,[8] it seems acceptable on *a priori* grounds alone that such limitations are beneficial in themselves regardless of what other factors may be at work in the situation. But if we accept the thesis that the objective of fisheries management is to raise the net economic yield of a fishery, our analysis is not complete until we have examined the effect of the programme on costs as well as on population and landings.

In Figure 9, the establishment of a catch ceiling is shown. Let us suppose that prior to this the fishery had been exploited beyond the optimum to the point where no net yield remained—with effort of Og as shown in the diagram. If the management authority could correctly determine the point of optimum effort and yield, it would set the catch ceiling at Oq, an amount which can be landed with Ox of fishing effort. But this catch limit is an aggregate one. The individual fishing unit is not formally limited in its catch. There is, then, created an inducement to individual fishermen to attempt to beat others to the limited supply of fish. This involves methods of fishing which are more costly. Larger

[8]See e.g., Martin D. Burkenroad, "Fluctuation in Abundance of Pacific Halibut," *Bulletin of the Bingham Oceanographic Collection*, vol. XI, May, 1948.

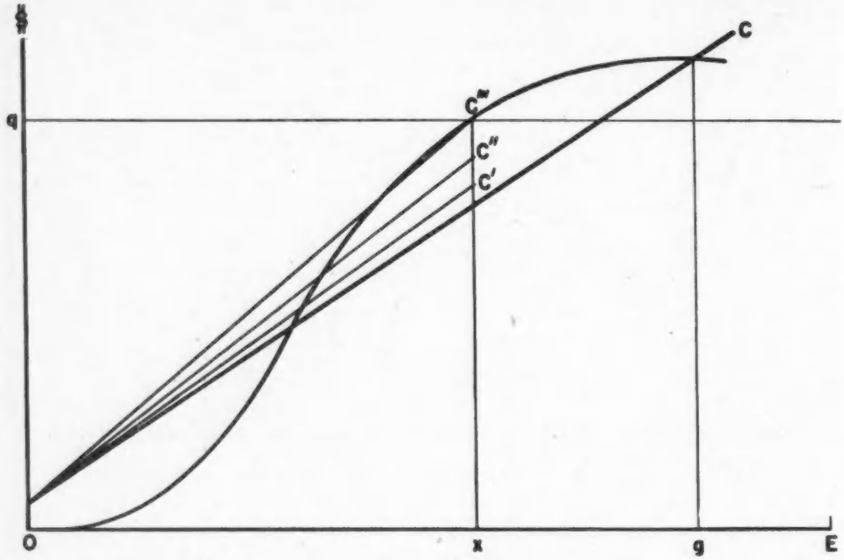

FIGURE 9

and faster boats are purchased in the competitive race for fish. The result is that the net yield that could have been obtained is dissipated through higher costs. The required fishing effort, Ox, is squeezed into a shorter and shorter period of time and the per-unit cost of fishing effort rises as shown by the rising slope of the cost function in Figure 9. There is no reason for this development to stop short of the point where the net yield of the fishery is again wholly dissipated.

In the case of the Pacific halibut fishery, these developments have taken place. Control brought about a considerable reduction in fishing effort, but larger and faster boats were built and the fishing season became shorter and shorter. Estimates indicate that the halibut population has risen substantially since control, and although it is not clear that control was the principal cause of this, it does not really matter, for costs have simply risen as well. There is no unequivocal evidence that the incomes of fishermen have benefitted. Catch limitations can only accomplish this broader objective if they are in the form of limitations on the catch of individual fishing units and are accompanied by restriction in the number of units that can engage in the fishery. Needless to say, such restrictions would be difficult to accomplish and would offend against political and social sensibilities that possess a high degree of acceptance in our society.

Seasonal limitations fare no better on this score. They formally lower the duration of fishing, but competition among fishermen takes the form of increasing the amount or effectiveness of fishing effort. In some cases the total catch is not reduced at all, but the costs of fishing are increased and the potential net yield is again dissipated. In the lobster fishery of the Maritime Provinces, for example,

seasonal closures have not restricted total catch, for it is generally conceded that a very high proportion of the available stock of lobsters is annually taken. The size of trap fleets has however grown very large, numbering several hundred per boat in some areas. In a few districts, fishermen have combined to limit their numbers and to reduce the size of trap fleets with consequent improvement to their incomes. This amounts to turning the lobster resource into private property and eliminating unproductive competition among its users. That it is successful is due to the fact that it strikes at the very heart of the overexploitation problem. This is, of course, much easier to accomplish with a relatively immobile species like the lobster than it would be with sea species like halibut, cod or haddock.

In general, the conclusion reached by this analysis is that an approximation to the optimum level of fishing effort can be achieved only under four kinds of conditions. (1) the resource may be divided into private property rights, as in oyster culture. The leasing of these to individual fishermen would promote rational utilization. (2) Where this is not possible, the resource can be given the status of *group* private property and exploited by the unified and co-ordinated action of its owners. (3) If neither of these is possible, the resource can be declared to be public property, and its exploitation governed, in specific detail, by public authority. (4) A taxation system could be devised that would reduce fishing effort on particular grounds to the optimum point. The proceeds of the tax could, of course, be redistributed to the fishermen, if desired.